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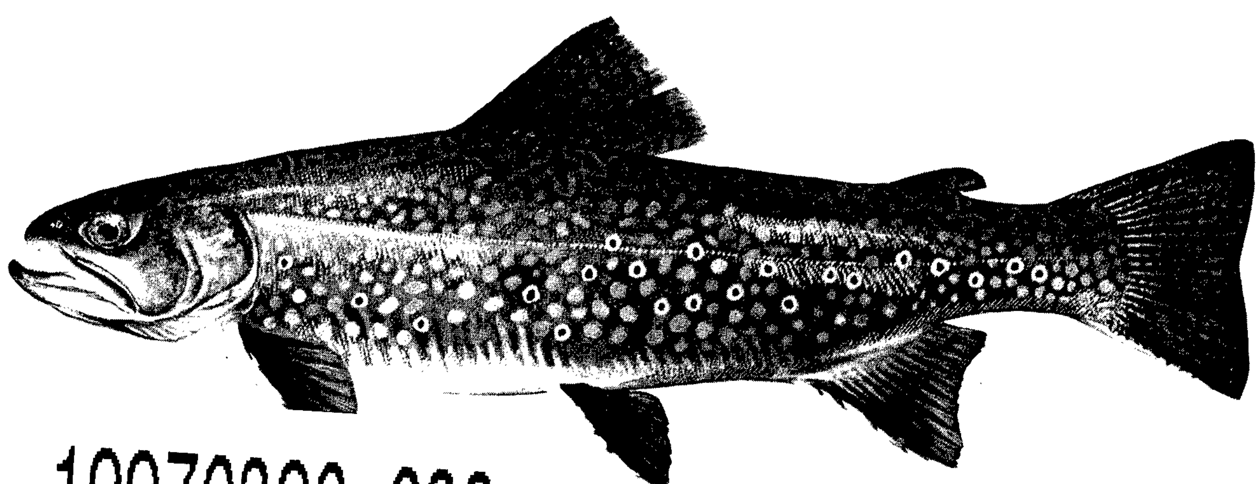
Habitat Suitability Index Model for Brook Trout in Streams of the Southern Blue Ridge Province: Surrogate Variables, Model Evaluation, and Suggested Improvements



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By

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Habitat Suitability Index Model for Brook Trout in Streams of the Southern Blue Ridge Province: Surrogate Variables, Model Evaluation, and Suggested Improvements

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Abstract. Data from several sources were collated and analyzed by correlation, regression, and principal components analysis to define surrogate variables for use in the brook trout (*Salvelinus fontinalis*) habitat suitability index (HSI) model, and to evaluate the applicability of the model for assessing habitat in high-elevation streams of the southern Blue Ridge Province (SBRP). In all data sets examined, pH and alkalinity were highly correlated, and both declined with increasing elevation; however, the magnitude of the decline varied with underlying rock formations and other factors, thereby restricting the utility of elevation as a surrogate for pH. In the data sets that contained biological information, brook trout abundance (as biomass, density, or both) tended to increase with elevation and decrease with the abundance of rainbow trout (*Oncorhynchus mykiss*), and was not significantly correlated ($P > 0.05$) with the

abundance of most benthic macroinvertebrate taxa normally construed as important in the diet of brook trout. Using multiple linear regression, we formulated an alternative HSI model—based on point estimates of gradient, pH, elevation, stream width, and rainbow trout density—which explained 40–50% of the variance in brook trout density in 256 stream reaches. Although logically developed, the present U.S. Fish and Wildlife Service HSI model, proposed in 1982, seems deficient in several areas, especially when applied to SBRP streams. We recommend that the water quality component in the model be updated and reevaluated, focusing on the differential sensitivities of each life stage, the stochastic nature of the water quality variables, and the possible existence of habitat requirements that differ among brook trout strains.

Key words: Alkalinity, benthos, brook trout, ecology, pH, rainbow trout, southeastern United States, streams, substrate.

The southern Blue Ridge Province (SBRP), an area of the Southern Appalachian Mountains comprising parts of western North Carolina, eastern Tennessee, northeastern Georgia, and extreme northwestern South Carolina, represents the southern limit of the original distribution of the brook trout (*Salvelinus fontinalis*) in North America (MacCrimmon and Campbell 1969; Fig. 1). The high-elevation streams of the SBRP constitute a peninsula of coldwater habitat that is surrounded by warmer waters harboring a diverse and potentially competitive ichthyofauna. Competition from introduced salmonids, particularly rainbow trout (*Oncorhynchus mykiss*), is especially problematic for fishery managers, and has been well documented (King 1937; Lennon and Parker 1959, 1967; Kelly et al. 1980; Moore et al. 1983, 1986; Silsbee and Larson 1983; Larson and Moore 1985; Fausch 1988). Studies completed to date indicate that brook trout of the SBRP are confined to high-elevation streams because of higher temperatures and the presence of competing species at lower elevations. The taxonomic status of the Southern Appalachian strain of brook trout is

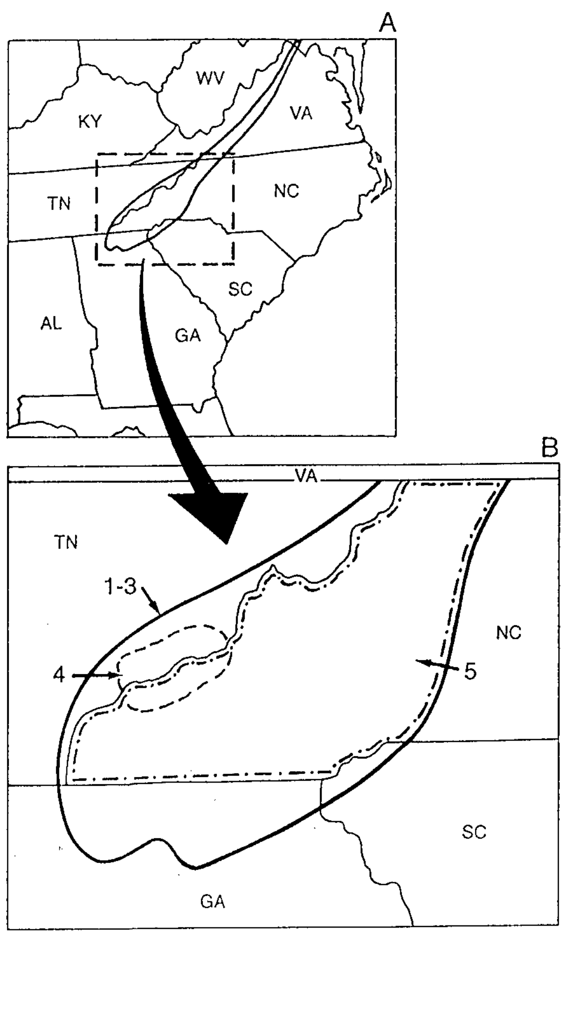

Fig. 1. Geographic location of the Blue Ridge Province (A) and southern Blue Ridge Province (B) in the southeastern United States. Areas covered in the original studies that provided data sets for this report are: 1–3 = southern Blue Ridge Province (Fowler 1985; Lasier 1986; Winger et al. 1987); 4 = Great Smoky Mountains National Park (C. R. Parker, unpublished manuscript, "Brook trout habitat in the Great Smoky Mountains National Park," archived 1988 at U.S. National Park Service, Great Smoky Mountains National Park, Gatlinburg, Tenn. [Parker MS]); 5 = state of North Carolina (North Carolina Wildlife Resources Commission 1983).

also an issue. Some researchers contend that it is taxonomically distinct, constituting a discrete subspecies (Lennon and Parker 1967); however, genetic studies (Stoneking et al. 1981; McCracken et al. 1993) still have not resolved this question.

The U.S. Fish and Wildlife Service habitat suitability index (HSI) model for brook trout (Raleigh 1982) incorporates several variables that, when applied to streams of the SBRP, are directly related to elevation. These variables include temperature (V_1, average maximum water temperature during the warmest period of the year; and V_2, average maximum water temperature during embryo development), as well as variables related to gradient and substrate (V_5, average water velocity over spawning areas during embryo development; V_7, average substrate particle size in spawning areas; V_9, dominant substrate type in riffle-run areas; and V_{16}, percent fines in riffle-run and spawning areas during average summer low flows), water chemistry (V_{13}, annual maximal or minimal pH), and stream size (V_4, average thalweg depth). Values for some of these variables are difficult, if not impossible, to obtain without intensive sampling and frequent observations. Our major objective was to explore relations among these variables and such readily obtainable information as stream size, order, gradient, and elevation to determine whether some of the more easily measured features can be used as surrogate variables for application of the brook trout HSI model in the SBRP. Our second objective was to evaluate the overall applicability of the model for brook trout in SBRP streams.

Methods

Considerable data are available for the high-elevation streams of the SBRP (Fig.1). Winger et al. (1987) surveyed physicochemical conditions in 30 SBRP headwater streams (point samples taken in first- and third-order reaches in each stream) during 1983–84 to determine their sensitivity to acidic deposition. The streams were selected on the basis of elevation (third-order reaches above 600 m), degree of human disturbance in the watershed, and accessibility. Fowler (1985) and Lasier (1986) studied a subset of the streams surveyed by Winger et al. (1987). They measured the physical and chemical attributes of several representative reaches (100 m per reach) in each of seven brook trout streams as determinants of benthic diversity and biomass (number and biomass per square meter), and of the fish assemblages of the streams (sampled with single-pass electrofishing). Staff of the North Carolina Wildlife Resources Commission (NCWRC 1983) surveyed 265 streams (representative 100-m reaches) in the SBRP for physicochemical attributes, benthic organism density (numbers of animals of major taxa per square foot), and fish community composition (single-pass electrofishing); brook trout were present in 143 of these streams. Biologists of the U.S. National Park Service (Park Service) also surveyed coldwater stream reaches in the Great Smoky Mountains National Park. From these data, the Park Service attempted to define regression models relating the abundance of brook trout and rainbow trout (single-pass electrofishing) to several habitat variables (Parker MS).[1]

For our investigation, existing data from the cited studies were collated and standardized where possible. Exploratory regression and correlation analyses were performed on each data set to determine the utility of the surrogate variables as predictors of the more difficult-to-measure physicochemical attributes (maximum temperatures, water quality variables, substrate particle size distributions, and velocity) and the biological variables (benthic biomass and brook trout abundance). Data for the primary dependent variables (brook trout density and biomass, alkalinity) were transformed ($\log_{10}$) to improve the linearity of predictions from the regression equations. At least two sets of regression analyses were performed for each data set that contained fish data: The relation of brook trout abundance, as density or biomass, was first analyzed against physicochemical variables for streams in which brook trout, but no introduced salmonids, were present, to determine whether abundance can be predicted on the basis of habitat factors alone. Another analysis included all variables to determine whether additional effects can be predicted by information on the abundance of other salmonids and whether predictive capability can be increased. A forward-selection, stepwise multiple regression procedure was used to fit the models. Variables were added to the model provided that the reduction in the unexplained sum-of-squares resulting from the addition was significant ($P < 0.05$). Other regression–correlation analyses were performed as needed to identify specific relations within individ-

[1] Parker, C. R. Unpublished manuscript. Brook trout habitat in the Great Smoky Mountains National Park. Archived 1988 at U.S. National Park Service, Great Smoky Mountains National Park, Gatlinburg, Tenn. 81 pp.

ual data sets and among combined data sets. Tabular summaries of the data sets and of the statistical analyses undertaken are presented in the Appendix.

Results

Initial analyses focused on simple correlations among biological and physicochemical variables. For those sets that contained fish data, the analyses then assessed predictive regression models that were generated for brook trout density and standing stock.

Winger et al. (1987)

Winger et al. (1987) studied first- and third-order stream reaches at elevations of 421–1,560 m, pH values of 4.41–7.14, and alkalinities of 0–204 μeq/L (Table A1). These streams drain watersheds underlain or influenced by three major classes of rock: (1) "crystalline complex" rocks—early Precambrian metamorphic and granitic gneisses and schists, including in some areas an overlay of later Precambrian sedimentary and metamorphic rock—which provide little buffering capacity and underlie slightly acidic, low-alkalinity streams; (2) glacial alluvium, which provides relatively high buffering capacity and underlies streams of moderate alkalinity and nearly neutral pH; and (3) the Anakeesta Formation, which is pyritic rock capable of producing acidity (Table A1). Because the underlying rock so profoundly influences water quality (Winger et al. 1987), separate correlation and regression analyses were performed for each of the three groups of streams, as well as for all streams combined.

In the 52 stream reaches underlain by the crystalline complex, pH and alkalinity were highly correlated ($P < 0.01$; Table A2). The correlation between elevation and pH was also significant ($P < 0.05$), but not that between elevation and alkalinity. In streams draining glacial alluvium, elevation, pH, and alkalinity were not significantly correlated; however, the sample size ($n = 4$) was small. In contrast, all correlations were significant ($P < 0.01$) in streams on the Anakeesta Formation, despite the small ($n = 6$) sample size. Stream order was not significantly correlated ($P > 0.05$) with any other variable in any of the three sets of streams. Inspection of the data revealed that the streams draining the Anakeesta Formation constituted a group distinct from the remainder of the streams, whereas those underlain by glacial alluvium did not (Fig. 2). Accordingly, two sets of regression equations, one for Anakeesta streams and one for the rest, were developed. For Anakeesta streams, the relations

$$\text{pH} = 11.598 - 0.005 \text{ elevation, and}$$
$$\log_{10}(\text{alkalinity}) = 5.018 - 0.003 \text{ elevation}$$

were highly significant ($P < 0.01$) and accounted for 85 and 74% of the variation in pH and alkalinity. For the remainder of the streams, the relations

$$\text{pH} = 6.982 - 0.0004 \text{ elevation, and}$$
$$\log_{10}(\text{alkalinity}) = 2.098 - 0.0003 \text{ elevation}$$

were also highly significant ($P < 0.01$) and accounted for 15 and 11% of the variability in pH and alkalinity (Fig. 2). These findings indicate that, for streams affected by the Anakeesta Formation, mean pH at base flow (as reported by Winger et al. 1987) can be predicted satisfactorily with knowledge of elevation. However, for the remainder of the streams, more information would be required, perhaps in the form of more precise data on bedrock geology.

Winger et al. (1987) reported that there was little difference in the acid-neutralizing capacity of the major formations constituting the crystalline complex. However, relations depicted in Fig. 2 indicate that there are subgroups within this larger grouping—suggesting that, with more information on bedrock geology and soil type, more accurate regression models might be developed.

Accordingly, to determine if better predictive models for pH and alkalinity can be produced by further stratification, the underlying rock formations and soil types constituting the watershed of each stream surveyed by Winger et al. (1987) were identified from information contained in geologic and soil maps (Stuckyey 1958; Hardman et al. 1966; Tennessee Valley Authority 1968; Pickering and Murray 1976). Regression analysis produced statistically significant ($P < 0.05$) relations for pH versus elevation in streams underlain by four of the six rock formations (including Anakeesta) for which data were adequate to warrant analysis (Table A3). Three of the six regressions were significant for the alkalinity–elevation regressions. Stratifying the streams according to their respective soil classifications also produced significant relations for the Porters–Ashe–Perkinsville and Ramsey–Ranger–Talledega soil groups, which together accounted for

60 of the 62 reaches surveyed (Table A4). Further stratification of the data to geologic and soil classifications provided little improvement over the regressions produced by the geologic stratification alone (Table A5); in the strata with sufficient data, the relations for the two stratification schemes were essentially identical (cf. Tables A3 and A5).

U.S. National Park Service

Of the three data sets that contain information on brook trout, the one based on survey data provided by the Park Service (Parker MS) summarized the most information on physical attributes of streams. The Park Service field records included observations on variables associated with geophysical and chemical characteristics (elevation, gradient, temperature, and pH); canopy coverage; bank composition (rocks, vegetation, and gravel); stream size (mean depth, mean wetted-area width, and mean channel width); in-stream cover (turbulence, rock, ledge, debris, vegetation, depth, bank, and total); substrate composition (organic debris, organic muck, sand, fine gravel, coarse gravel, small rubble, large rubble, boulder, bedrock, and silt); woody debris (stability, length, and volume); and pool area. The data were collected during 1984 and 1986 (Table A6). The Park Service also determined the density of brook trout and rainbow trout in each stream reach.

As expected, there were significant correlations among physicochemical measurements and many of the habitat descriptors in the combined (all-years) data set (Table A7). Midsummer temperature, pH, canopy coverage, stream size, rock cover, substrate, fine gravel, and substrate boulder abundance were all negatively correlated with elevation, whereas in-stream debris cover, substrate sand and bedrock, and total woody debris increased with elevation. Brook trout density was positively correlated with elevation and bank vegetation and negatively correlated with measurements of rainbow trout density, temperature, pH, in-stream bedrock, width, and in-stream boulders. In contrast, rainbow trout density was negatively correlated with elevation, bank vegetation, in-stream debris, and substrate fine gravel and silt, and was positively correlated with stream size and in-stream rocks and boulders. Most of these associations support the general assumptions of the brook trout HSI model.

The two sets of multiple regression analyses that we performed on the combined (1984 and 1986) Park Service data each produced models that provided excellent predictions of brook trout density. For streams containing brook trout but no introduced salmonids, statistically significant models containing the variables elevation, pH, bank vegetation, stream width, pool area, and amount of debris present explained as much as 87% of the variation in brook trout density (Table A8). When all streams containing brook trout were analyzed, models that included physicochemical variables and negative coefficients for rainbow trout density explained 77% of the variance in brook trout density.

As noted by Parker (MS), the streams of the Great Smoky Mountains National Park differed substantially between 1984 and 1986; 1984 was a "normal" water year, whereas the summer of 1986 was marked by near-record drought conditions and unusually low water levels. Regression analyses performed independently on the two sets of data yielded different and often contradictory relations. Although both sets of relations accurately predicted brook trout density within the data sets from which they were derived (R^2 = 0.91 to 0.99 for 1984, 0.87 to 0.97 for 1986; Table A8), cross-validation failed to uphold the relations; the 1984 models could not satisfactorily predict the 1986 abundance of brook trout (based on 1986 data for the independent variables), and the 1986 model fared poorly when applied to the 1984 data. The models were contradictory in that different variables were selected for each year, and the coefficients for some variables had opposite signs in the two models. Parker (MS) concluded that the two sets of samples were essentially drawn from different "populations" (in the statistical sense).

Fowler (1985) and Lasier (1986)

Fowler (1985) and Lasier (1986) studied a subset of the streams investigated by Winger et al. (1987) throughout the SBRP. Although the data subset assessed fewer physicochemical variables (stream width, depth, flow, gradient, elevation, pH, and alkalinity) than the Park Service analysis (Parker MS), habitat coverage was expanded by incorporating extensive density and biomass estimates for fishes and invertebrates (Table A9). In the expanded data subset, brook trout density and biomass were negatively correlated with rainbow trout density and biomass to about the same degree as in the Park Service data (cf. Tables A7 and A10). Brook trout abundance was also negatively correlated with the abundance of sculpins (*Cottus* spp.) and brown trout (*Salmo trutta*), and with several physicochemical variables (stream width, depth, and flow). Width, depth, and flow were negatively

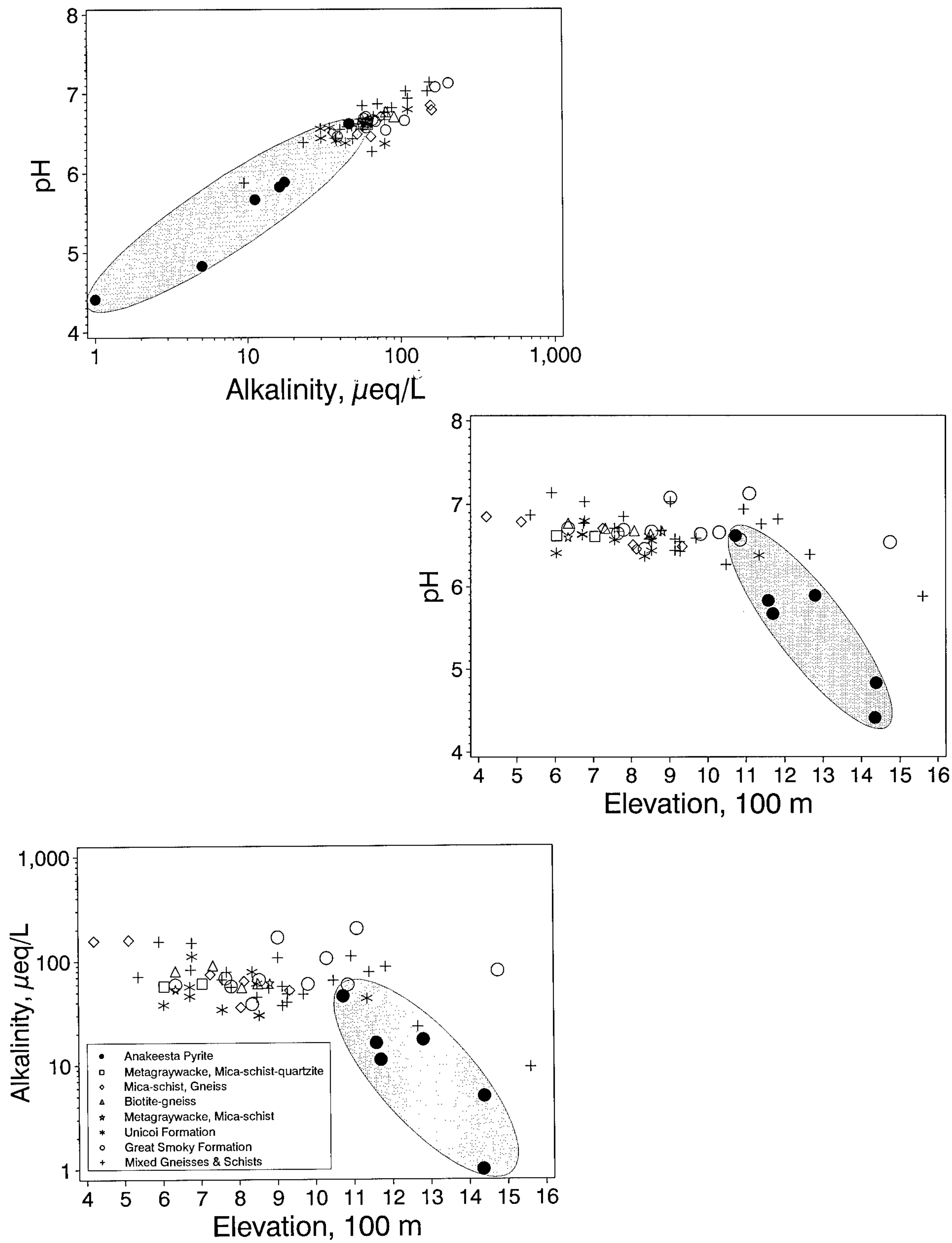

Fig. 2. Relations among pH, alkalinity, and elevation in 62 headwater stream reaches of the southern Blue Ridge Province surveyed by Winger et al. (1987) underlain by (1) the Anakeesta Formation (*solid circles bounded by shaded ellipses*) and (2) other geologic formations and rock types.

correlated with elevation, whereas the correlation of elevation with pH was positive (Table A10). As in the data from Winger et al. (1987), of which Fowler's (1985) data are a subset, pH and alkalinity were also positively correlated (Table A10).

Among the aquatic invertebrates included by Lasier (1986), the abundance of those representing the insect orders Odonata, Ephemeroptera, Plecoptera, Trichoptera, and Diptera (taxa important in the diet of brook trout; Tebo and Hassler 1963; Reed and Bear 1966; Cada et al. 1987) were positively correlated with at least one measure of stream size (order, width, or depth; Table A10). Only the abundance of plecopterans was correlated with elevation, and the coefficient was negative. The abundance of coleopterans, which often are important in salmonid diets, was positively correlated with elevation. Brook trout density and biomass were negatively correlated (albeit weakly) with the abundance of Odonata and Diptera, whereas the biomass and density of the other fishes present in the streams were positively correlated with the abundance of invertebrates representing several taxa. Collectively, these findings indicate that benthic invertebrates are less abundant in the upper reaches of the streams, where the brook trout are most abundant, than in the lower reaches, which are more heavily populated by competing species. The findings also indicate that benthic invertebrate abundance has little effect on the distribution or abundance of brook trout. However, the relations among total available food, the specific organisms actually being consumed (preferred food), and number of preferred feeding locations in the stream reaches were not determined. The abundance of visually isolated feeding lanes that deliver preferred food items in drift may be as important for the production of salmonids as the total amount of invertebrate food available in the stream (Chapman 1966; Dolloff 1983). Thus, the neutral and negative correlations between brook trout density and benthic invertebrate abundance might simply indicate that there are relatively few preferred feeding areas in small, high-elevation streams.

For the data from Fowler (1985) and Lasier (1986), stepwise multiple regression analysis using only physicochemical variables produced models that explained about 70% of the variation in brook trout abundance (density and biomass) in streams containing no competing salmonids (Table A11). When the analyses were expanded to include biological variables and streams containing competing salmonids, models containing physicochemical variables, a term for gastropod abundance, and negative terms for rainbow trout and either sculpin or brown trout abundance explained as much as 87% of the variance in brook trout abundance.

North Carolina Wildlife Resources Commission

Stream survey data gathered by the North Carolina Wildlife Resources Commission (NCWRC 1983) also contained information on benthic invertebrates and fishes (Table A12). In this data set, brook trout density was positively correlated with elevation and in-stream cover, and negatively correlated with pH, stream length, width, and flow (Table A13). Among the biological variables, brook trout abundance was positively correlated with the abundance of Odonata (opposite of the association for Fowler's data), and negatively correlated with the abundance of rainbow trout and other fishes, and three benthic taxa—Ephemeroptera, Coleoptera, and Trichoptera. Alkalinity and pH were positively correlated and, as reported for the data of Winger et al. (1987), both variables declined with increasing elevation. The abundance of Ephemeroptera and Coleoptera in the North Carolina survey data was negatively correlated with elevation and positively correlated with pH and alkalinity, as reported for Fowler's (1985) and Lasier's (1986) data. Other benthic taxa were positively correlated with variables related to stream size, corroborating the finding of greater benthic organism density in the lower reaches of these streams, where brook trout coexist with other fishes.

Multiple regression analyses with the NCWRC survey data yielded models that explained less variability than models derived from the other data sets. For brook trout streams only, a model containing measurements of width, flow, pH, and cover explained 39% of the variance in brook trout density (Table A14). For all streams, a model containing three physicochemical variables and negative terms for rainbow trout, brown trout, striped jumprock (*Moxostoma rupiscartes*), and Megaloptera density, and a positive term for Odonata density, explained about 59% of the variance in brook trout density.

Commonalities and Cross-validation

To provide some degree of cross-validation, we combined all three data sets discussed above. Only six variables—brook trout density, rainbow trout density, gradient, elevation, pH, and stream width—were common to all three data sets. Be-

cause many of the other variables in each data set were correlated with the six common variables (Tables A7, A10, and A13), multiple regression analysis was used to fit linear, quadratic, and cubic terms in five independent variables for the combined data set. For all streams (n = 256), a model containing positive terms for elevation, gradient (quadratic), and stream width (cubic), and negative terms for gradient (linear and cubic) and width (quadratic), explained 48% of the variation in brook trout density (Table A15). Examination of the residuals for this relation revealed that, although the fit of the model was good given the heterogeneous data sources, there was strong positive bias on the low end. Moreover, the model failed to predict the absence of brook trout in the presence of rainbow trout, and it overestimated brook trout abundance despite the inclusion of a negative cubic term for rainbow trout. When the analysis was restricted to brook trout streams (those containing brook trout but no rainbow trout; n = 165), a model that included positive terms for elevation (linear) and gradient (quadratic), and negative terms for pH (linear) and stream width (quadratic), explained 44% of the variability in brook trout density. The model for brook trout only was also biased positively on the low end despite the deletion of the streams containing rainbow trout and those not containing brook trout from the analysis; however, there was no apparent pattern to the deviations with respect to data source (i.e., none provided a discrete cluster). Therefore, there was no demonstrated effect of locale and method of data collection.

Evaluating Competition Between Brook Trout and Rainbow Trout

Because brook trout have food and space requirements that are similar to those of other stream-dwelling fishes, the other species are often viewed as direct competitors in situations where the availability of food or other habitat components seems to be limited. Competition, particularly with rainbow trout, is strongly implicated as a regulatory mechanism for brook trout in the SBRP (Larson and Moore 1985). Moreover, a reduction in density and biomass of brook trout has been attributed to summer food limitation in SRBP streams where brook trout and rainbow trout occur (Ensign et al. 1990). To examine competitive displacement, we computed the total abundance of fishes other than brook trout for each stream reach in those data sets containing species information (by NCWRC [1983] and Fowler [1985]). We determined correlations among total fish abundance (all species other than brook trout combined), brook trout abundance and density, and rainbow trout abundance.

In the reaches studied by Fowler (1985), the negative correlations between brook trout density and biomass and the corresponding abundance of all other species combined (Table A16) were virtually identical to the correlations between brook trout and rainbow trout abundance (Table A10). Similarly, total fish abundance correlated to about the same extent as rainbow trout abundance with the physicochemical attributes of the streams (cf. Tables A10 and A16). In the NCWRC data, the correlations for total fish abundance (Table A17) were slightly greater than for any single species, including rainbow trout (Table A13). These slight differences probably reflect the much broader array of streams and habitats surveyed by the NCWRC. Collectively, our results indicate that rainbow trout exert as great an influence on brook trout as all other species combined and lend support to the contention that rainbow trout are key competitors with brook trout in the SBRP. However, the weak to negative relation of brook trout biomass to abundance of food organisms (Tables A10–A13) argues against food limitation on a broad scale. The mechanisms by which rainbow trout and other species exert competitive influences do not seem to center on direct competition for food. Spatial factors regulating the availability of preferred foods, such as the number of visually isolated feeding lanes per unit of stream, may be a more important competitive mechanism than the absolute amount of food available (Dolloff 1983). The HSI model considers dominant substrate type (V_9; assumption that substrate containing most abundant aquatic insects is optimum), thalweg depth (V_4), pool class (V_{15}), and in-stream cover (V_6), but does not include a measure of the spatial or temporal associations between these or other variables that define preferred feeding habitat. The development and inclusion of a variable describing the availability of preferred feeding locations would be useful to assess the potential foraging competition in streams where rainbow trout are present.

Discussion

Some of the variables in the brook trout HSI model (Raleigh 1982) are at best nebulously defined. As noted by Trial et al. (1984), the where, when, and how to measure and compute variables

are not specified, such as for minimum dissolved oxygen concentration (V_3), average maximum daily temperatures during different life stages (V_1 and V_2), average thalweg depth (V_4), average velocity (V_5), and average annual minimum or maximum pH (V_{13}); moreover, the methods used to obtain these data may profoundly affect their values. Hence, the major hypothesis to be tested by our investigation was that at least some of these variables can be predicted on the basis of more readily available information. Our findings indicate that for SBRP streams these predictions can be made, but only to a limited extent. Many variables were correlated with elevation, as expected. On the other hand, our analysis of the data from Winger et al. (1987) showed that pH, an especially significant variable, could not be predicted satisfactorily for streams draining all rock and soil types. Therefore, we note that there are important limitations in utility of the surrogate approach.

Another problem with pH is that minima in streams are typically episodic, that is, associated with runoff events (snowmelt and periods of intense rainfall) that typically depress the acid-neutralizing capacity of SBRP streams by 17–29% (Messer et al. 1988). Mean and minimal values are not independent, however, because buffering capacity (i.e., alkalinity) declines with base pH (Fig. 2A). Consequently, streams with low pH at base flow characteristically experience the widest pH excursions during the year. This phenomenon is well illustrated in Table 1 of Winger et al. (1987), which reveals a much greater coefficient of variation for hydrogen ion activity and alkalinity in streams of low pH. Other evidence indicates that such pH excursions are toxic to brook trout in streams based on the Anakeesta Formation and that pH acts in concert with other water quality constituents, especially metals, to exert its toxicity in acidic streams of the SBRP (Huckabee et al. 1975).

Despite the inherent problems outlined above, our analysis of the individual and combined data sets indicated that brook trout habitat quality can be predicted on the basis of point estimates of pH and variables that can be obtained from maps and aerial photographs. This proposal reflects accumulated point estimates of population density and, for Fowler's (1985) data, standing stock estimates of biomass (Tables A8, A11, A14, and A15). The combined data could be used to assign a suitability index of 1.0 to streams with the greatest brook trout densities and zeros to those in which no brook trout were found; the equations in Table A15 become, with all variables except pH $\log_{10}$ transformed,

$$\text{HSI} = 0.22 - 0.78\,(\text{gradient}) + 2.08\,(\text{gradient})^2 - 1.21\,(\text{gradient})^3 - 0.07\,(\text{pH}) + 0.11\,(\text{elevation})^2 - 0.17\,(\text{width})^2 - 0.007\,(\text{rainbow trout density})^2$$

for all streams, and

$$\text{HSI} = 0.18 + 0.52\,(\text{elevation}) - 0.15\,(\text{pH}) - 0.19\,(\text{width})^3 + 0.06\,(\text{gradient})^2$$

for streams containing brook trout and no rainbow trout. Despite the obvious bias of the models (Fig. 3), these "HSI" values are correlated to a greater degree with brook trout abundance ($r^2 = 0.6$ to 0.7) in the 256 SBRP stream reaches included in this exercise than were the values derived from the original HSI model (Raleigh 1982) by Trial et al. (1984) in their attempt to validate the HSI model for Maine streams ($r^2 < 0.5$).

In studies of brook trout-habitat relations in Wyoming, Chisolm and Hubert (1986) and Kozel and Hubert (1989) found that brook trout abundance increased with elevation and decreased with stream size. Kozel and Hubert (1989) also reported that brook trout biomass declined as the abundance of brown trout increased. These findings were corroborated in all of our analyses for brook trout in the SBRP. In our three sets of test data containing information on brook trout (and in the combined analysis), brook trout abundance was positively correlated with elevation but declined with increasing stream size and rainbow trout abundance. Kozel and Hubert (1989), citing their own and other studies, also noted that such determinants of habitat quality as overhead vegetation, width-to-depth ratio, and the abundance of pools with in-stream cover increased with elevation but declined with stream size. Therefore, the empirical data indicate that abiotic and biotic factors must be considered when predicting brook trout density and biomass. The surrogate variables identified in our analysis focus on environmental factors that determine habitat structure and water quality (gradient, pH, elevation, and width), as well as potential competitive interactions (rainbow trout density).

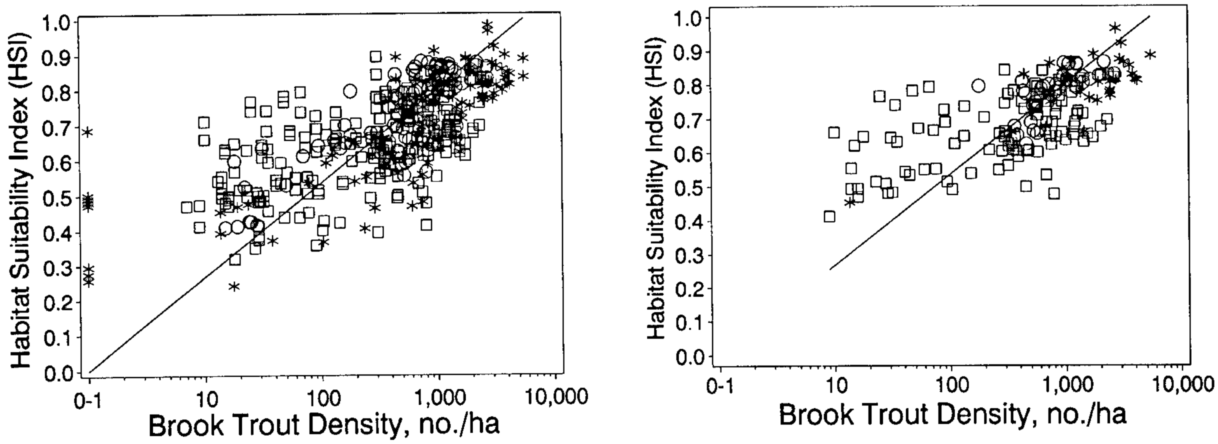

Fig. 3. Habitat suitability index (HSI = 100 × predicted standing stock / maximum standing stock) versus measured standing stock in streams of the southern Blue Ridge Province. *Diagonal lines* represent perfect agreement between HSI and measured standing stock; *circles* = surveys by Fowler (1985); *squares* = surveys by the North Carolina Wildlife Resources Commission; *asterisks* = surveys by the U.S. National Park Service (Parker MS). *Upper panel*: all streams (n = 256); *lower panel*: brook trout (*Salvelinus fontinalis*) streams, no rainbow trout (*Oncorhynchus mykiss*) present (n = 172).

Limitations of the Regression–Correlation Approach and Comparison With Principal Components Analysis

The use of multiple regression models that assume linear, additive relations among environmental (i.e., habitat) variables and animal abundance can be misleading, primarily because species tend to have an optimum level for each variable (Green 1977). Examination of the suitability curves in the brook trout HSI model illustrates clearly that this fact was recognized by Raleigh (1982), and it is the reason that nonlinear terms were considered in the combined regression analyses in our study. Similar studies of salmonid abundance–habitat relations characteristically include only linear terms or, at best, log-transformed variables (e.g., Binns and Eiserman 1979; Chisolm and Hubert 1986; Wesche and Goertler 1987; Kozel and Hubert 1989).

The assumption of additivity in the multiple regression approach usually precludes allowances for interactions among habitat variables. Although such interactions are implicit in the brook trout HSI model through its aggregation procedures, multiple regression assumes pure additivity. Other investigators have resolved this problem by testing combinations of selected pairs of variables (e.g., Orth and Maughan 1982). Although useful for small numbers of variables, this approach is not practicable for large numbers of variables or where interactions are not suspected a priori. Alternatively, a multivariate approach that seeks out latent variables within the set of environmental variables (e.g., by factor or principal components analysis), combined with regression, can sometimes resolve this complex problem (e.g., Morrison 1967). To test this hypothesis, principal components (scores), as linear combinations of the habitat variables, were computed for each set of independent variables in the combined data set. We then tested these values to determine their ability to predict brook trout abundance. For the combined data set, this approach produced HSI values that were correlated to a lesser degree with brook trout density than were the values produced by regression analysis (cf. Tables A18–A20).

Another drawback of HSI validation by correlation–regression analysis is that the approach is based on single point estimates of temporally fluctuating dependent and independent variables (Platts and Nelson 1988). As noted by Cumbie and Gnilka (1990), trout populations are influenced by ecosystem productivity, interactions with other species, harvest, and other factors that lie beyond the

measurable physical habitat. Also implicit in the regression–correlation approach is the assumption that changes in habitat produce an instantaneous population response; that is, there can be no time lag or delayed response. The data analyzed in our study, especially those of the Park Service (Parker MS), illustrate these problems. The three brook trout data sets showed the influence of other species (especially rainbow trout) that, along with the gradient of habitat characteristics, also changed with elevation. We can only speculate as to the extent and significance of sport fishing on the brook trout and rainbow trout densities measured in the studies from which our data came. We do know, however, that the accessibility of SBRP streams generally declines with increase in elevation, further confounding the habitat assessment.

Our cross-validation problems with the Park Service data (models based on 1984 data did not accurately predict conditions observed in 1986) also clearly illustrated the effects of temporal variation on apparent correlations between habitat and species abundance, and the possible influence of compensatory lag. Another example was provided by a recent study of brook trout streams in South Carolina (Cumbie and Gnilka 1990) where, in two physically similar streams, HSI was 0.68–0.76 for brook trout and 0.74–0.76 for rainbow trout. Although these values indicate high-quality habitat for both species in both streams, one stream contained no fishes at all as a result of logging and other past disturbances in the watershed from which the stream had not yet recovered. Obviously, a correlation–regression validation based on point estimates in such disturbed habitat would prove futile, as would any other approach.

Problems in Application of HSI Models to Brook Trout in the Southern Blue Ridge Province and to Stream-dwelling Fishes in General

Implicit in the HSI approach is the assumption that high-quality habitat supports (or can support) a high biomass of the species in question and low-quality habitat supports low biomass. Although appealing in its simplicity, the approach presents several problems when applied to fishes, especially in streams.

The change in the characteristics of trout populations with distance from the headwaters reflects longitudinal zonation (Hynes 1972) or longitudinal succession (Sheldon 1968; Cummins 1972; Hawkes 1975), for which streams are noted. This zonation forms the basis of the river continuum concept (Vannote et al. 1980). A stream, by definition, is a habitat continuum that, for brook trout, is often reflected in a productivity continuum. This productivity continuum derives from the lower space requirements of small salmonids than of large salmonids (Chapman 1966; Allen 1969); the greater efficiency of small fishes than of large fishes in the conversion of food to biomass (Brett et al. 1969); the presence of fewer competing species in upstream reaches, especially in the SBRP; and the fact that a unit area of small stream contains proportionately more usable habitat and riparian vegetation than a larger one (Kozel and Hubert 1989). The "steepness" of the habitat continuum (i.e., the rate of longitudinal succession) is a property of the stream that needs to be determined as part of the habitat assessment process. Moreover, if biomass is the index of species performance selected to assess habitat suitability, two units of habitat in different streams can be compared only if they are at equivalent points along their respective habitat continua. Without accounting for position on the continuum, a biomass-oriented index for salmonids will invariably lead upstream, toward small streams populated by large numbers of small trout. Resource managers are not likely to accept such an index; a recent survey showed that fisheries professionals consider fish size to be an important determinant of stream fishery value (Angermeier et al. 1991).

The steepness of the habitat continuum for streams supporting brook trout is highly variable. In streams of the SBRP, the habitat continuum changes rapidly because of several factors. One major force governing water quality and stream ecology in this region is climate, which is itself a component of the habitat continuum. Climate in the SBRP varies greatly with elevation. In the lowlands (elevation 450–500 m) it is warm and humid, with an average rainfall of about 150 cm / year and an average temperature of about 13.5° C. The climate is progressively cooler and wetter with increase in elevation; at about 2,000 m it is classified as either "perhumid" or "rain forest," with an average annual temperature of 7.6° C and average rainfall of >230 cm/year (Shanks 1954). Lennon and Parker (1967) noted that climate had a profound effect on brook trout in the Great Smoky Mountains National Park; at higher elevations the streams flowed near bankfull for most of the rainy spring, summer, and fall, but many redds were exposed and some froze

during the winter low-flow period. Anchor ice was viewed as especially hazardous for developing embryos and overwintering adults and juveniles owing to the highly variable winter temperatures and resultant freeze-thaw cycles, which periodically allow the ice to break loose and scour the streambeds. In contrast, streams at lower elevations in the park are characterized by spring flow maxima and late summer-early fall minima, and streams do not generally freeze (Parker MS). The increasing severity of the winter conditions with elevation may also explain the corresponding decline—though not necessarily interdependence—in benthic productivity and success of rainbow trout noted in the data we analyzed. Rapid changes in the habitat continuum make uniform application of a single HSI model for brook trout difficult in the SBRP, a factor true for many other stream fish-habitat models that have been examined (Fausch et al. 1988).

To be used successfully, HSI models for stream fishes must incorporate, and thereby predict, the primary factors responsible for density, biomass, and production (i.e., population regulators). The identification of these limiting factors for brook trout in the SBRP has been particularly elusive because of the wide spatial and temporal fluctuations in habitat conditions (steepness of the habitat continuum), and the lack of empirical data documenting the relative importance of individual habitat components (e.g., large woody debris, thalweg depth, spawning substrates). In other areas of the country, the success of stream habitat improvement programs in increasing standing stock and production has demonstrated the importance of "habitat" as a limiting factor in brook trout populations (e.g., Hunt 1969, 1976). At least some of the success of these programs has been achieved through an increase in the adult overwintering survival rate rather than through any increase in recruitment or growth (Hunt 1969). Survival to the adult stage is generally perceived as density dependent and indirectly controlled by the habitat (McFadden et al. 1967; McFadden 1969). Competition by adults for limited spawning areas may result in fry survival rates that vary inversely with spawning population density, having lower fry survival in marginal spawning areas during periods of high density than in more suitable areas during periods of both low and high density (McFadden et al. 1967). In other instances recruitment has been shown to be independent of parental stock density (McFadden 1969). Population regulation, where it occurs, is often achieved through emigration enforced through territoriality, with the size of the territory varying in proportion to the available food supply (primarily invertebrate drift) and the amount of visual isolation provided by the habitat's heterogeneity (Chapman 1966). These factors operate simultaneously, however, and the primary density regulator may change seasonally.

Seasonal fluctuation in what seem to be primary density regulators is particularly problematic for accurate assessment of overall habitat suitability. Food may be limiting through its effect on territory size during spring, summer, and early fall, whereas habitat suitability—in terms of protection from predation, displacement, and physical damage—may be limiting in winter (Chapman 1966). In regions where streams may have excessively high summer water temperatures, low water levels, or both, the quantity of suitable summer habitat (in the form of shaded seepages) may be limiting. Although V_8 (substrate size) of the HSI model addresses winter cover for fry and juveniles, variables V_4 (thalweg depth) and V_6 (in-stream cover) specifically address "the late growing season, low-water period," thereby assuming warm-season habitat limitation for adults. In the higher elevations of the SBRP, however, winter habitat may be in short supply (Lennon and Parker 1967), as has been demonstrated elsewhere (Hunt 1969). Moreover, it would be difficult to estimate the amount of winter (i.e., low-water) habitat present based on a field reconnaissance conducted during the warmer seasons of higher flow; conducting low-water surveys and estimating conditions at higher flows would be easier. Winter conditions may also limit the reproductive success of brook trout at higher elevations in the SBRP (Lennon and Parker 1967).

The HSI model of Raleigh (1982) represents a logically constructed summary, based on recent literature and expert opinion, of the mechanisms and factors that control the abundance of brook trout. No attempt was made to standardize methods of data acquisition for habitat variables in the model. Consequently, as noted by others (Trial et al. 1984), some variables exist only in theory; in practice, many either cannot be determined or are at best stochastic, indicating that they would be better addressed in probabilistic than in absolute terms. Other variables may best be termed determinants of habitat, rather than habitat per se. In this context, we equate habitat with what others

term microhabitat (e.g., Orth and Maughan 1982). Among the habitat determinants are such variables as discharge, stream size (e.g., width), gradient, cover, canopy, and substrate, which in turn dictate water velocity, depth, turbulence, and incident light intensity. These variables define the number of suitable, visually isolated territories that a unit of stream contains. Stream fishes typically segregate along habitat continua formed by these variables and their heterogeneity (e.g., Gibson and Keenleyside 1966), which are in turn determined by primary factors such as stream size and substrate (as well as by proportions typically measured by stream biologists—woody debris, rocks, boulders, vegetation, overhead cover, riffle–pool ratio, etc.). The tendency of stream biologists to focus on variables that are habitat determinants might at least partly explain why the models developed from Park Service data for two different water years (Parker MS) could not be cross-validated, and why HSI models developed for other fishes (e.g., Layher and Maughan 1985, 1988; Layher et al. 1987) have generally fared poorly in tests of geographic cross-validation.

According to Chapman's (1966) "grand speculation," salmonids in streams are governed primarily by spatial requirements, with the size of the required space varying indirectly with the food supply and directly with the size of the individuals. Thus, the first task in quantifying habitat would seem to be the determination of the habitat requirements (in terms of space and characteristics) of the species in question; to some extent, space requirements are a strict function of fish size, even among different salmonid species (Allen 1969). The second task would be to determine the amount of suitable space (i.e., meeting the requirements of the species) present in the stream under consideration. This approach forms the basis of the "instream flow incremental methodology" (Stalnaker 1979; Orth and Maughan 1982), another means of stream habitat quantitation employed by the U.S. Fish and Wildlife Service. The habitat requirements also vary with the presence or absence of other species (e.g., Fausch and White 1981, 1986), which also must be considered.

Conclusions and Recommendations

1. Brook trout habitat assessment in the SBRP needs to be scaled for the position of a particular reach in the stream habitat continuum. Even with the obvious limitations imposed by regression–correlation analysis, trends in habitat with elevation were apparent. With increasing elevation, SBRP streams generally decreased in size, pH, alkalinity, average size of the brook trout present, and benthic productivity. Conversely, brook trout standing stock and density increased with elevation. Nevertheless, fishery managers probably would not accept an index that favored small streams supporting small trout over large streams supporting large fish. For this reason, and given the steepness of the habitat continuum in the SBRP, position along the continuum must be standardized by stream order and elevation when comparisons are made.
2. The present brook trout HSI model (Raleigh 1982) seems to be biased towards regions of the United States where warm-season habitat is limiting. In contrast, in the SBRP (and probably elsewhere), survival through the winter may be limiting (Lennon and Parker 1967). Although recognized in the model documentation (Raleigh 1982:4–5), the variables used in the application of the model assume late growing-season extremes. Clearly, the HSI model user should be instructed to identify and select appropriate limiting factors, which vary geographically and seasonally, as part of the method of application.
3. Our results indicate that benthic invertebrate food organisms (abundance and biomass) may not be an important limiting factor for brook trout in SBRP streams. Conditions that determine the abundance of preferred foods and feeding locations (associations between V_4, V_6, V_{11}, V_{15}, and V_{16}) are probably more important than the total amount of food available (implicit in V_7 and V_8). The aggregation procedure used in the 1982 HSI model must be refined to include new variables (and new combinations of existing variables) to more precisely define preferred foraging habitat. Relations between total food availability (terrestrial and aquatic origin), food selection, and availability of preferred feeding habitats (and their proximity to other required habitat components) must be evaluated for use in the model. Integrated variables that describe an optimal spatial arrangement of habitat elements associated with feeding (as well as spawning, rearing, and overwintering) would be more useful than several loosely asso-

ciated determinants of foraging habitat, as is now the case.

4. The results of this study and many others before it (in the SBRP and elsewhere), as well as laboratory studies (Fausch and White 1981, 1986), have shown that the carrying capacity of streams for brook trout is reduced by the presence of other salmonids. Although a manager can theoretically reduce or eliminate these competitors through a rigorous removal program, such as that practiced in the Great Smoky Mountains National Park (Moore et al. 1983, 1986; Larson and Moore 1985), total eradication is seldom possible (e.g., Lennon and Parker 1959), repopulation by the unwanted species is inevitable, and continuing control is necessary. For streams of the SBRP, our regression analyses might be used to estimate the improvement likely to result from a given level of rainbow trout control. The technique might also be useful for determining the amount of effort necessary to mitigate the loss of brook trout from streams where encroachment by rainbow trout has occurred and restoration is desirable.
5. In the context of HSI model application, the stochastic nature of the water quality variables (i.e., dissolved oxygen, pH, and temperature), as well as those related to water quantity (thalweg depth, velocity, riffle–pool structure, etc.), is particularly problematic. These variables fluctuate temporally, and absolute minima and maxima are extremely difficult or impossible to measure. Instead, they are often couched in probabilistic terms such as "10-year low flow" and "100-year flood." Yet within the present brook trout HSI model, only V_{14} (flow variation) is probabilistic; the other variables are expressed in absolute terms, to be modified by V_{14} (and the rest of the variables in the "other" component) during the aggregation process. Users of the model should be aware of the inherent difficulty in obtaining accurate measurements for the variables that the model expresses in absolute terms (primarily V_1–V_5 and V_{13}). In reality, the measurements may more closely resemble point estimates rather than absolute maxima or minima, which leads to compounded error in the final HSI calculation.
6. The water quality component of the model ignores several basic tenets of aquatic toxicology. The duration of exposure to potentially harmful conditions (temperature, dissolved oxygen, pH, etc.) is as important in determining the outcome of the exposure as the level of the stress itself, as is the pre-exposure history of the organism (i.e., the acclimation period), which means that tolerance varies seasonally. Although some of this time-related reasoning is incorporated in current water quality regulations (e.g., U.S. Environmental Protection Agency [EPA] 1985), the variables constituting the water quality component of the HSI model are stated only as annual absolutes (minimum, maximum). A better approach might be to adopt, where possible, existing levels and limits proposed as water quality criteria for the protection of aquatic life (EPA 1985, 1986), which are stated in statistical terms (mean levels during specified periods). Of course, the use of such an approach requires far more data than the point estimates implicitly specified for use in the present HSI model.
7. Another shortcoming of the water quality component of the brook trout HSI model is that it is now badly out of date. Since publication of the model in 1982, the interrelations of salmonids and water quality (especially pH and related variables) have been studied intensively in response to heightened public awareness of acidic precipitation and its consequences. Among the most important recent findings are the substantial differences in sensitivity among the life stages of brook trout and other salmonids to water quality conditions, and the interactions between pH and other water constituents in determining the outcome of exposure (e.g., Cleveland et al. 1986; Jagoe et al. 1986, 1987). We recommend that more recent material be reviewed and incorporated into a revised version of the water quality component of the HSI model. The revised model also should evaluate the utility of the approaches described previously for dealing with stochastic variables, and should treat each life stage separately. Such precise information would be especially valuable to fishery managers contemplating mitigation through watershed liming or habitat improvement, where any increases in yield per unit of improvement would depend on water quality.
8. The HSI model was developed for uniform application to brook trout populations wherever they occur or to habitats where they were historically found. The model allows for spatial variation in habitat components but assumes one important constant—that there is no geo-

graphic variation in brook trout populations or their response to habitat conditions. Information on life history characteristics and morphology (Lennon and Parker 1967; McGlade and MacCrimmon 1979) and studies of population genetics (Stoneking et al. 1981; McCracken et al. 1993) indicate that the Southern Appalachian strain of brook trout is taxonomically distinct. Lennon and Parker (1967) noted the failure of attempts to repopulate Great Smoky Mountains National Park streams with brook trout derived from northern strains, whereas fish of Southern Appalachian origin did well. These findings indicate that water quality requirements of brook trout from the Southern Appalachian strain differ from those of northern strains; however, requirements of northern brook trout form the basis of literature and laboratory standards on brook trout habitat requirements. For cutthroat trout (*Oncorhynchus clarki*), significant among-strain differences in sensitivity to pH and associated water quality variables have been demonstrated (Woodward et al. 1991). In sum, the existence of interstrain differences in the context of HSI model application for brook trout may be important, but remains to be evaluated.

9. The five surrogate variables that were identified in our study (gradient, pH, elevation, width, and rainbow trout density) more precisely explained brook trout abundance in 256 stream reaches in the SRBP than did the original HSI model. Moreover, brook trout abundance was more closely correlated with these surrogate variables than were the values derived from the original model when applied to streams in Maine (Raleigh 1982). In practical terms, use of the surrogate variables may provide substantial savings in costs of equipment and personnel for gathering data necessary to evaluate brook trout habitat in the SBRP; moreover, their use would increase the precision of estimates. It is important to stress, however, that accuracy of the surrogate variables in predicting brook trout abundance, biomass, or responses to habitat restoration or other management actions in the SRBP must be validated in the field before the approach can be widely implemented. We recommend that the water quality component of the original HSI be revised to reflect current information on pH effects and related variables, and that the refined model be compared with surrogate variables by field-testing in the SBRP.

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Appendix. Statistical Tables

Table A1. Mean ($\bar{x}$), standard deviation (SD), minimum, and maximum values of variables determined by Winger et al. (1987) for reaches of 30 streams of the southern Blue Ridge Province (SBRP) underlain by three types of rock.

Bedrock geology and statistic	Stream order	Elevation (m)	pH[a]	Alkalinity (μeq/L)[a]
Crystalline complex (n = 52)[b]				
$\bar{x}$	2.0	876.1	6.62	59.02
SD	1.0	208.2	0.20	32.92
Minimum	1	536.0	5.88	9.50
Maximum	3	1,560.0	7.13	204.52
Glacial alluvium (n = 4)[c]				
$\bar{x}$	2.0	550.3	6.95	154.88
SD	1.1	109.4	0.16	4.16
Minimum	1	421.0	6.79	150.00
Maximum	3	677.0	7.14	159.40
Anakeesta pyrite (n = 6)[c]				
$\bar{x}$	1.8	1,259.3	5.54	9.49
SD	1.0	152.9	0.80	16.14
Minimum	1	1,073.0	4.41	0.0
Maximum	3	1,439.0	6.62	46.00
All types (n = 62)[c]				
$\bar{x}$	2.0	892.1	6.54	52.60
SD	1.0	244.7	0.45	41.14
Minimum	1	421.0	4.41	0.0
Maximum	3	1,560.0	7.14	204.52

[a] Values for pH and alkalinity are based on the means of 5–6 observations per reach.
[b] Contains early Precambrian metamorphic gneisses and schists overlain in some areas by later Precambrian sedimentary and metamorphic rock.
[c] Geometric mean.

Table A2. Statistically significant[a] correlations (Pearson product-moment, r) between variables in reaches of 30 SBRP streams underlain by three types of rock. Data from Winger et al. (1987).

Bedrock geology and variable	pH	Alkalinity[b]
Crystalline complex[c] (n = 52)		
Elevation	-0.31*	-0.18
pH		0.81**
Glacial alluvium (n = 4)		
Elevation	0.68	-0.80
pH		-0.70
Anakeesta pyrite (n = 6)		
Elevation	-0.92**	-0.86**
pH		0.97**
All (n = 62)		
Elevation	-0.60**	-0.57**
pH		0.93**

[a] $^{**}P \leq 0.01$; $^{*}P \leq 0.05$.
[b] As $\log_{10}$ of value.
[c] Per Table A1, footnote b.

Table A3. Results of regression analyses fitting equations of the form $y_i = \beta_0 + \beta^1 x_i$, where y_i = either pH or alkalinity and x_i = elevation, to the data of Winger et al. (1987) after grouping the streams according to underlying rock formations (numbers in parentheses represent key to data and headings in Tables A4 and A5).

Variable and formation	n	F[a]	R^2	β_0	β_1	$\bar{x}$
pH						
Anakeesta pyrite (0)	6	23.17**	0.85	11.599	-0.0048	5.54
Glacial alluvium (1)	4	1.9	0.49	6.386	0.0010	6.95
Crystalline complex[b]	52	5.32*	0.10	6.892	-0.0003	6.24
Mica schist-gneiss (2)	6	25.34**	0.86	7.198	-0.0012	6.64
Biotite-gneiss (3)	4	119.85**	0.98	7.133	-0.0006	6.70
Unicoi Formation[c] (6)	10	2.47	0.24	6.891	-0.0004	6.54
Great Smoky conglomerates[d] (8)	11	0.01	<0.01	6.743	-0.0001	6.71
Mixed gneisses and schists[e] (9)	21	15.32**	0.45	7.410	-0.0008	6.67
All except Anakeesta Formation	56	9.88**	0.15	6.982	-0.0004	6.65
Alkalinity, µm/L ($\log_{10}$)						
Anakeesta pyrite (0)	6	11.19*	0.74	5.018	-0.0032	0.98
Glacial alluvium (1)	4	3.49	0.64	2.237	-0.0001	2.19
Crystalline complex	52	1.74	0.03	1.933	-0.0001	1.77
Mica schist-gneiss (2)	6	16.44**	0.80	2.728	-0.0012	1.89
Biotite-gneiss (3)	4	2.36	0.54	2.429	-0.0008	1.85
Unicoi Formation (6)	10	0.29	0.03	1.867	-0.0002	1.69
Great Smoky conglomerates (8)	11	1.08	0.11	1.595	-0.0003	1.89
Mixed gneisses and schists (9)	21	14.21**	0.43	2.461	-0.0007	1.78
All except Anakeesta Formation	56	6.70*	0.11	2.098	-0.0003	1.80

[a] df = 1, $n - 1$; *$P \leq 0.05$, **$P \leq 0.01$.
[b] Includes all except glacial alluvium and Anakeesta Formation.
[c] Sandstones, quartzites, conglomerates, shales, and slates.
[d] Graywacke sandstone and conglomerate with slate interbeds.
[e] Mica gneiss, mica schist, and other gneisses and schists.

Table A4. Results of regression analyses fitting equations of the form $y_i = \beta_0 + \beta_1 x_i$, where y_i = either pH or alkalinity and $\bar{x}_i$ = elevation, to the data of Winger et al. (1987) after grouping the streams according to watershed soil type (codes in parentheses for formations and soil types as in Table A3).

Variable and soil type	n	F^a	R^2	β_0	β_1	$\bar{x}$
pH						
Porters–Ashe–Perkinsville (1)[b]	32	25.69**	0.46	7.345	-0.0009	6.60
Ramsey–Ranger–Talladega (2)[c]	28	13.12**	0.34	7.856	-0.0014	6.46
Alkalinity ($\log_{10}$)						
Porters–Ashe–Perkinsville (1)	32	27.83**	0.48	2.420	-0.0008	1.74
Ramsey–Ranger–Talladega (2)	28	6.85*	0.21	2.475	-0.0009	1.66

[a] df = 1, n -1; *$P \leq 0.05$, **$P \leq 0.01$.
[b] Level terrain; parent material alluvium.
[c] Mountainous terrain; parent materials gneiss, schist, and granite.

Table A5. Results of regression analyses fitting equations of the form $y_i = \beta_0 + \beta_1 x_i$, where y_i = either pH or alkalinity and $\bar{x}_i$ = elevation, to the data of Winger et al. (1987) after grouping the streams according to underlying rock formations and watershed soil types

Variable and geologic formation/ soil codes[b]	n	F^a	R^2	β_0	β_1	$\bar{x}$
pH						
0/2	5	24.16**	0.89	12.044	-0.0051	5.12
2/1	4	2.08	0.51	7.318	-0.0009	6.54
3/1	4	119.85**	0.98	7.133	-0.0006	6.70
6/2	10	23.97**	0.59	7.428	-0.0009	6.63
8/2	11	2.47	0.24	6.891	-0.0004	6.54
9/1	19	0.01		6.743	-0.0001	6.71
Alkalinity						
0/2	5	10.20*	0.77	5.335	-0.0034	0.96
2/1	4	0.30	0.13	2.215	-0.0006	1.74
3/1	4	2.36	0.54	2.429	-0.0007	1.85
6/2	10	0.29	0.04	1.867	-0.0002	1.69
8/2	11	1.08	0.11	1.595	-0.0003	1.89
9/1	19	20.27**	0.54	2.483	-0.0008	1.75

[a] df = 1, n -1; *$P \leq 0.05$, **$P \leq 0.01$.
[b] Codes for formations and soil types as in Tables A3 and A4.

Table A6. Mean ($\bar{x}$), standard deviation (SD), median, minimum, and maximum values of variables measured in 71 stream reaches (n = 70 for debris characteristics) in Great Smoky Mountains National Park by the U.S. National Park Service (Parker MS).[a]

Variable	$\bar{x}$	SD	Median	Minimum	Maximum
Physicochemical					
Elevation (m)	1,051.7	249.2	1,037.0	433	1,488
Gradient (%)	8.9	4.9	8.0	2.0	24.0
Temperature (° C)	14.8	2.3	15.0	9.0	18.0
pH	6.1	0.31	6.1	5.6	6.8
Mean depth (cm)	16.9	9.9	12.9	4.1	49.1
Stream width (m)	5.0	2.0	4.7	2.0	11.3
Channel width (m)	8.8	3.4	8.0	3.4	18.9
Canopy (%)	69.9	18.9	75.0	0	100.0
Bank composition (%)					
Rock	51.0	29.4	50.0	0	95.0
Vegetation	40.0	28.9	45.0	0	91.0
Gravel	6.5	8.8	5.0	0	30.0
In-stream cover (%)					
Turbulence	15.2	9.0	13.9	1.2	38.6
Rock	9.3	6.0	8.1	0.6	30.2
Ledge	1.4	2.2	0.5	0	10.5
Debris	2.1	2.6	1.3	0	13.3
Vegetation	1.8	4.5	0.1	0	31.9
Depth	2.1	3.3	1.0	0	19.9
Bank	0.5	1.1	0	0	6.2
Total	32.3	14.9	30.6	9.4	76.2
Substrate composition (%)					
Organic debris	2.6	2.8	1.9	0	15.6
Organic muck	0.3	0.7	0	0	3.8
Sand	7.7	7.0	5.4	0	25.2
Fine gravel	16.2	11.0	15.4	0	59.2
Coarse gravel	10.9	6.4	9.6	0	26.8
Small rubble	12.0	6.3	11.1	0.5	30.0
Large rubble	10.7	7.2	9.4	0	39.4
Boulder	29.0	15.0	26.3	2.2	66.3
Bedrock	9.2	17.4	1.1	0	71.6
Silt	1.2	2.0	0.6	0	11.9
Debris characteristics					
Stability index[b]	12.4	2.8	12.6	4.9	17.0
Total length (km / ha)	6.3	5.3	4.6	0	19.8
Total in-stream (km / ha)	1.5	1.6	0.8	0	6.9
Log volume (m^3/ ha)	31.0	53.9	10.7	0	287.0
Associated debris (m^3/ ha)	345.0	781.4	73.0	0	4,073.0
Total volume (m^3/ ha)	376.0	782.2	103.0	0	4,087.0
Fish density (no. / ha)					
Brook trout[c]	1,136.5	1,244.1	740.4	0	5,538.9
Rainbow trout[d]	352.3	524.6	0	0	2,141.2
Total pool area (%)	38.8	16.0	38.0	6.0	74.0

[a] Parker, C. R. Unpublished manuscript. Brook trout habitat in the Great Smoky Mountains National Park. Archived 1988 at U.S. National Park Service, Great Smoky Mountains National Park, Gatlinburg, Tenn. 81 pp.

[b] Dimensionless indicator of permanence.

[c] *Salvelinus fontinalis.*

[d] *Oncorhynchus mykiss.*

Table A7. Statistically significant[a] correlations between variables measured by the U.S. National Park coefficients above the principal diagonal (indicated by *bullets*), Spearman rank coefficients below.

	General					Bank composition		
	Elevation	Gradient	Temperature	pH	Canopy	Rock	Vegetation	Gravel
General								
Elevation	•	—	-0.61	-0.31	-0.24	—	—	—
Gradient	—	•	—	—	—	—	—	-0.40
Temperature	-0.60	—	•	—	—	—	—	-0.02
pH	-0.36	—	—	•	—	—	—	—
Canopy	-0.27	—	—	—	•	—	—	—
Bank composition								
Rock	—	—	—	—	—	•	-0.78	—
Vegetation	—	—	—	—	—	0.86	•	-0.23
Gravel	—	-0.43	—	—	—	—	—	•
Stream size								
Depth	—	-0.33	—	—	—	0.37	-0.48	0.30
Wetted width	-0.25	-0.34	—	—	—	0.44	-0.44	0.31
Channel width	—	-0.22	—	—	—	0.51	-0.55	0.34
In-stream cover								
Turbulence	—	—	—	—	—	—	—	—
Rock	-0.21	—	—	—	—	—	—	—
Ledge	—	—	0.22	0.21	—	—	0.27	-0.43
Debris	0.25	0.32	—	—	—	-0.32	0.39	-0.35
Vegetation	—	—	—	—	—	-0.36	0.27	—
Depth	—	—	0.20	—	—	—	0.27	-0.45
Bank	—	—	—	—	—	—	—	—
Substrate composition								
Organic debris	—	—	—	—	-0.28	-0.30	0.25	-0.20
Organic muck	—	—	—	—	—	-0.22	—	—
Sand	0.21	0.24	—	—	—	-0.29	0.21	—
Fine gravel	-0.26	—	0.26	0.45	—	-0.34	0.50	-0.33
Coarse gravel	—	—	—	0.28	0.22	—	0.33	-0.23
Small rubble	—	-0.25	—	—	0.21	-0.21	—	0.34
Large rubble	—	-0.22	—	-0.22	—	-0.28	—	—
Boulder	-0.26	—	—	—	—	0.38	-0.42	—
Bedrock	0.31	—	—	—	—	—	—	—
Silt	—	-0.20	—	—	-0.22	—	-0.26	0.25
Miscellaneous habitat								
Total cover	—	—	—	—	—	—	—	—
Debris stability	—	-0.22	—	-0.37	—	—	-0.25	0.43
Total debris	0.24	—	—	-0.38	—	—	—	0.23
In-stream debris	—	—	—	—	—	-0.23	0.21	—
Log volume	—	0.36	—	—	—	-0.25	0.39	-0.46
Assoc. debris volume	—	—	—	-0.26	—	—	—	—
Total debris volume	—	—	—	—	—	—	—	—
Fish density								
Brook trout	0.63	—	-0.39	-0.22	—	-0.32	0.43	—
Rainbow trout	-0.51	—	0.29	0.36	—	0.40	-0.34	—
Total pool area	—	—	—	—	—	0.25	-0.21	—

[a] If $|r| \geq 0.30$, $P < 0.01$; if $0.30 > |r| \geq 0.23$, $P < 0.05$; if $0.23 > |r| \geq 0.20$, $P < 0.10$.

Service (Parker MS) in 71 streams of Great Smoky Mountains National Park. Pearson product-moment *Dashes* indicate pairs of variables not significantly correlated. Variables as in Table A6.

Stream size			In-stream cover						
Depth	Wetted width	Channel width	Turbu-lence	Rock	Ledge	Debris	Vege-tation	Depth	Bank
-0.24	-0.28	—	—	—	—	0.23	—	—	—
-0.31	-0.38	-0.23	—	—	—	0.27	—	—	—
—	—	—	—	—	0.24	—	—	—	—
—	—	—	—	0.27	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—
0.35	0.44	0.50	—	—	—	-0.33	-0.29	—	—
-0.43	-0.47	-0.58	—	—	0.32	0.39	—	0.27	—
0.24	0.30	0.30	—	—	-0.42	-0.34	—	-0.44	—
•	0.69	0.61	0.24	—	—	-0.41	—	—	—
0.59	•	0.87	—	—	—	-0.37	-0.20	—	—
0.57	0.85	•	—	—	—	-0.37	-0.25	-0.22	—
0.26	0.24	0.24	•	0.33	—	—	-0.22	0.34	—
—	—	—	0.33	•	0.28	—	-0.21	—	—
—	—	—	—	0.26	•	—	—	0.27	—
-0.43	-0.31	-0.34	—	—	—	•	0.20	0.23	0.20
—	—	-0.29	-0.25	-0.26	—	0.24	•	—	0.20
—	—	—	0.34	—	0.37	—	—	•	—
—	—	—	—	—	—	0.23	0.27	—	•
-0.32	-0.24	-0.26	—	—	0.28	0.54	0.35	—	—
—	-0.33	-0.23	—	—	—	0.35	0.34	—	—
-0.32	-0.40	-0.51	—	-0.34	—	0.52	0.33	—	—
-0.46	-0.37	-0.42	—	0.34	0.30	—	—	—	—
-0.59	-0.33	-0.31	—	0.29	—	0.28	—	—	—
—	—	—	—	—	-0.27	—	—	-0.37	—
0.22	—	—	—	—	—	—	—	—	0.25
0.38	0.27	0.45	0.21	0.44	—	-0.43	-0.33	—	—
—	—	—	—	—	—	—	—	—	—
0.21	—	—	—	—	—	—	—	—	—
—	—	—	0.75	0.61	0.31	0.22	—	0.55	—
0.52	—	—	—	-0.47	-0.40	—	—	-0.24	—
0.21	-0.22	—	—	-0.38	-0.27	—	—	—	—
—	—	-0.31	—	-0.32	—	0.22	—	—	—
0.41	-0.38	-0.54	-0.26	—	—	0.61	—	0.24	—
—	—	-0.23	—	-0.30	—	0.33	—	—	—
—	-0.36	-0.33	-0.21	-0.26	—	0.45	—	—	—
0.51	-0.48	-0.48	—	—	—	0.35	—	—	—
0.25	0.43	0.45	—	0.32	—	-0.26	—	—	—
0.31	—	—	0.27	—	—	-0.29	—	-0.28	—

Table A7. *Continued.*

Substrate composition									
Organic debris	Organic muck	Sand	Fine gravel	Coarse gravel	Small rubble	Large rubble	Boul-der	Bed rock	Silt
—	—	0.20	-0.23	—	—	-0.23	-0.27	0.34	—
—	—	0.20	—	—	-0.28	-0.25	—	—	—
—	—	—	0.35	0.23	—	—	—	—	—
	—	—	0.42	0.27	—	—	—	—	—
-0.20	-0.29	—	—	—	—	—	—	—	—
-0.32	-0.25	-0.29	-0.27	—	-0.24	-0.28	0.37	—	—
0.23	—	0.21	0.49	0.27	—	—	-0.45	—	-0.22
—	—	—	—	-0.20	0.34	—	—	—	0.24
-0.34	—	-0.32	-0.42	-0.44	—	0.26	0.34	—	—
-0.24	-0.28	-0.39	-0.30	-0.23	—	—	0.30	—	—
-0.21	-0.23	-0.47	-0.31	—	—	—	0.51	—	—
-0.20	—	—	-0.21	—	—	—	—	—	—
—	—	-0.30	0.40	0.36	-0.21	—	0.39	-0.34	—
0.23	—	—	0.33	—	-0.27	—	—	—	—
0.52	0.34	0.50	—	0.23	—	—	-0.39	—	—
0.31	0.34	0.34	—	—	—	0.21	-0.26	—	—
—	—	—	—	—	-0.36	—	—	—	—
—	—	—	—	—	—	—	—	—	—
•	0.42	0.46	0.22	—	—	—	-0.38	—	—
—	•	0.28	—	—	—	—	—	—	—
0.48	0.28	•	—	—	—	-0.24	-0.64	0.22	—
0.27	—	—	•	0.37	-0.25	—	—	-0.45	—
0.22	—	—	0.32	•	—	—	—	-0.55	-0.23
—	—	—	-0.23	0.20	•	0.32	—	-0.35	—
—	—	-0.23	—	—	0.25	•	—	-0.41	—
-0.43	-0.23	-0.64	—	—	—	0.24	•	-0.47	—
—	—	0.21	-0.28	-0.36	-0.31	-0.23	-0.35	•	—
—	—	—	—	—	—	—	—	—	•
—	—	—	—	—	—	—	—	—	—
—	—	—	-0.50	-0.54	0.25	0.32	—	0.21	0.29
—	—	0.21	-0.35	—	0.23	—	—	—	—
—	—	—	—	—	—	—	—	—	—
0.43	—	0.46	0.31	0.30	—	—	0.42	—	—
—	—	0.28	—	—	—	—	—	—	—
0.27	0.20	0.36	—	—	—	—	-0.23	—	—
0.22	—	0.26	0.25	—	—	-0.20	-0.47	—	—
—	—	-0.37	—	—	—	—	0.47	-0.28	—
-0.27	—	-0.24	—	-0.26	—	—	0.20	—	—

Miscellaneous habitat variables							Fish density		
Total cover	Debris stability	Total debris	In-stream debris	Log volume	Assoc. debris volume	Total debris volume	Brook trout	Rainbow trout	Total pool-area
—	—	0.26	—	—	—	—	0.62	-0.28	—
—	—	—	0.25	—	—	—	-0.23	—	—
—	—	—	—	—	—	—	-0.30	—	—
—	-0.34	-0.32	—	0.24	—	—	-0.25	0.24	—
—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	-0.27	-0.28	-0.36	0.42	0.25
—	-0.27	—	—	0.25	—	—	0.40	-0.44	—
-0.21	0.40	—	—	-0.28	0.28	0.26	—	—	—
—	0.43	—	—	-0.32	—	—	-0.38	0.27	0.29
—	—	-0.29	-0.22	-0.24	—	—	-0.44	0.49	—
—	—	-0.21	-0.23	-0.28	—	—	-0.41	0.54	—
0.76	—	—	—	-0.24	—	—	—	—	0.29
0.66	-0.49	-0.34	-0.26	—	—	—	—	0.28	—
0.32	-0.48	-0.22	—	—	—	—	—	—	—
0.27	—	—	—	0.44	0.22	0.25	0.20	-0.24	-0.33
—	—	—	—	—	—	—	0.20	—	—
0.57	-0.20	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—
—	—	—	—	0.33	—	—	—	-0.21	-0.27
0.23	—	—	—	—	0.23	0.24	0.24	—	—
—	—	—	—	0.38	—	—	—	-0.29	-0.21
—	-0.46	-0.33	—	—	—	—	0.21	—	—
—	-0.50	—	-0.21	0.29	—	—	—	—	-0.20
—	0.23	—	—	—	—	—	—	—	—
—	0.26	—	—	—	0.24	—	—	—	—
—	—	—	—	-0.31	—	—	-0.45	0.47	—
—	—	—	—	—	—	—	0.21	—	—
—	0.33	—	—	—	—	—	—	—	—
•	-0.27	-0.23	-0.22	—	—	—	—	—	0.21
-0.29	•	0.61	0.49	—	—	—	—	-0.20	—
—	0.67	•	0.82	0.30	0.41	0.43	—	-0.26	—
-0.23	0.47	0.77	•	0.30	0.42	0.44	—	-0.31	—
—	—	0.31	0.61	•	—	—	—	—	-0.29
—	0.31	0.71	0.60	0.43	•	>0.99	—	—	—
—	0.24	0.70	0.66	0.61	0.96	•	—	—	—
—	—	—	—	0.29	—	—	•	-0.48	—
—	-0.31	-0.30	-0.42	-0.30	-0.22	-0.25	-0.61	•	—
0.20	—	—	—	—	—	—	—	—	•

Table A8. Results of multiple regression analysis, as regression coefficients[a] and other statistics,[b] relating brook trout abundance (no./ha) to habitat variables (including the abundance of rainbow trout) in streams of Great Smoky Mountains National Park (Parker MS). Variables as defined in Table A6.

Regression statistics and variables	1984			1986[c]		1984 and 1986		
	Brook trout streams[d]	Trout streams[e]	All streams and data	Brook trout streams	Trout streams	Brook trout streams	Trout streams	All streams and data
n	16	27	34	17	36	33	63	70
R^2	0.99	0.93	0.91	0.97	0.87	0.85	0.76	0.76
F^b	129.23	73.01	45.58	55.21	32.88	25.15	29.33	33.86
Intercept (β_0)	-880.670	-359.672	-799.262	-9,457.060	-3,299.962	7,395.073	-1,566.343	-1491.316
Elevation	1.288	1.500	1.925	7.237	3.665	2.666	2.880	2.880
Canopy	-10.585	—	—	153.251	32.887	—	—	—
Bank rock	-10.665	-15.252	—	—	—	—	—	—
Small rubble	48.566	—	—	—	—	—	—	—
Large rubble	30.592	—	—	—	—	—	—	—
Total debris length	0.079	0.090	—	—	—	-0.190	—	—
Ledge cover	—	—	—	—	—	—	—	—
Sand	—	—	—	-52.375	—	—	—	—
Boulder	—	—	—	28.969	—	—	—	—
Debris stability	—	—	—	323.027	—	—	—	—
Log volume	—	—	—	-6.684	—	—	—	—
Depth cover	—	-211.655	—	—	—	—	—	—
Rainbow trout	—	—	-0.525	—	-1.363	—	-0.757	-0.712
Gradient	—	—	-52.375	—	-87.185	—	-86.606	-86.987
Coarse gravel	—	—	78.934	—	-58.288	—	—	—
Total pool area	—	—	—	—	20.330	44.483	23.678	22.372
Depth	—	—	—	—	—	—	-33.950	-31.775
Fine gravel	—	—	—	—	—	—	21.971	20.036
pH	—	—	—	—	—	-1,709.468	—	—
Bank vegetation	—	—	—	—	—	25.917	—	—
Channel width	—	—	-63.995	—	—			
Bank gravel	—	—	25.751	—	—	—	—	—

[a] All listed coefficients statistically significant ($P \leq 0.05$); *dashes* indicate pairs of variables not significantly correlated.
[b] All regressions highly significant overall ($P < 0.01$).
[c] All streams surveyed in 1986 contained trout.
[d] Distinguished by absence of rainbow trout.
[e] Distinguished by presence of rainbow trout.

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Table A9. Mean ($\bar{x}$), standard deviation (SD), median, minimum, and maximum values of variables as measured in seven SBRP streams (n = 56) by Fowler (1985).

Variable	$\bar{x}$	SD	Median	Minimum	Maximum
Physicochemical					
Order	1.9	1.0	1.0	1.0	3.0
Width (m)	3.8	2.1	3.2	1.1	10.1
Depth (cm)	22.0	7.9	21.5	8.0	35.0
Flow (cubic feet / s)	4.8	8.0	2.0	0.1	32.2
Gradient (%)	10.8	3.7	10.9	2.4	17.1
Elevation (m)	900.6	137.5	878.0	658.0	1,170.0
pH	6.64	0.18	6.6	6.4	7.0
Alkalinity (mg / L)	2.95	1.43	2.4	1.5	5.6
Fish abundance[a]					
Brook trout					
Adult density	660.5	559.5	532.5	15	2,693.0
Adult biomass	13.6	12.0	10.5	0.1	46.0
Y-O-Y[b] density	179.0	729.0	0	0	5,427.0
Y-O-Y biomass	0.4	1.5	0	0	10.9
Rainbow trout					
Adult density	222.6	326.4	0	0	1,173.0
Adult biomass	6.4	10.0	0	0	38.7
Y-O-Y density	42.8	118.6	0	0	661.0
Y-O-Y biomass	0.2	0.6	0	0	3.6
Brown trout[c] density	5.5	26.0	0	0	151.0
Brown trout biomass	0.9	3.2	0	0	15.2
Longnose dace[d] density	31.0	95.8	0	0	478.0
Longnose dace biomass	0.4	1.3	0	0	5.9
Creek chub[e] density	4.1	30.7	0	0	230.0
Creek chub biomass	0.1	0.3	0	0	2.3
Sculpin[f] density	308.8	575.7	0	0	2,115.0
Invertebrate density[g]					
Oligochaeta	9.0	8.9	5.0	0	36.0
Gastropoda	0.02	0.13	0	0	1.0
Odonata	3.2	3.1	2.0	0	14.0
Ephemeroptera	50.6	47.6	35.5	3.0	173.0
Plecoptera	20.3	10.1	20.0	6.0	38.0
Coleoptera	3.4	2.9	3.0	0	11.0
Megaloptera	0.02	0.13	0	0	1.0
Trichoptera	12.6	7.7	11.0	3.0	31.0
Diptera	30.3	24.9	20.5	4.0	121.0

[a] Fish density = no. / ha; biomass = kg / ha.
[b] Young of the year.
[c] *Salmo trutta.*
[d] *Rhinichthys cataractae.*
[e] *Semotilus atromaculatus.*
[f] *Cottus* spp.
[g] Invertebrate density = no. / m^2.

Table A10. Statistically significant[a] correlations between variables in seven SBRP streams ($n = 56$) (indicated by *bullets*), rank coefficients below. *Dashes* indicate pairs of

Variable	Physicochemical variables							
	Order	Width	Depth	Flow	Gradient	Elevation	pH	Alkalinity
Physicochemical								
Order	•	0.71	0.72	0.55	−0.55	−0.58	—	—
Width	0.77	•	0.78	0.85	—	−0.70	—	−0.27
Depth	0.72	0.84	•	0.57	—	−0.65	—	—
Flow	0.87	0.82	0.76	•	—	−0.58	—	—
Gradient	−0.48	−0.27	—	—	•	—	—	—
Elevation	−0.56	−0.68	−0.64	−0.58	—	•	0.29	0.52
pH	—	—	—	0.29	—	—	•	0.86
Alkalinity	−0.26	−0.46	0.39	−0.30	−0.23	0.66	0.51	•
Fish abundance								
Brook trout								
Adult density	−0.52	−0.57	−0.46	−0.46	0.49	0.50	—	—
Adult biomass	−0.50	−0.59	−0.42	−0.41	0.61	0.37	—	—
Y-O-Y density	—	—	—	—	—	—	0.34	—
Y-O-Y biomass	—	—	—	—	—	—	0.34	—
Rainbow trout								
Adult density	0.54	0.45	0.37	0.38	−0.45	−0.57	−0.36	−0.38
Adult biomass	0.58	0.49	0.41	0.45	−0.42	−0.60	−0.34	−0.40
Y-O-Y density	0.45	0.35	0.28	0.40	−0.39	−0.45	−0.30	−0.29
Y-O-Y biomass	0.46	0.36	0.30	0.42	−0.38	−0.46	−0.30	−0.29
Brown trout density	0.31	0.31	0.25	0.36	—	−0.37	−0.32	—
Brown trout biomass	0.31	0.31	0.25	0.36	−0.25	−0.38	−0.32	−0.23
Longnose dace density	0.42	0.45	0.46	0.47	—	−0.57	−0.24	−0.35
Longnose dace biomass	0.42	0.45	0.47	0.47	—	−0.57	−0.24	−0.35
Creek chub density	—	—	—	—	−0.23	—	—	—
Creek chub biomass	—	—	—	—	−0.23	—	—	—
Sculpin density	0.45	0.34	0.25	0.24	−0.63	−0.28	−0.37	−0.28
Sculpin biomass	0.47	0.36	0.28	0.26	−0.62	−0.28	−0.36	−0.28
Invertebrate density								
Oligochaeta	0.53	0.24	—	0.42	−0.37	—	—	—
Gastropoda	—	—	—	—	—	—	—	—
Odonata	—	—	—	—	—	—	−0.26	—
Ephemeroptera	0.24	0.37	0.38	0.36	0.27	—	—	−0.25
Plecoptera	0.38	0.38	0.31	0.44	—	−0.38	—	−0.39
Coleoptera	—	—	—	—	—	—	—	—
Megaloptera	—	—	—	—	—	—	—	—
Trichoptera	0.44	—	—	0.32	−0.23	—	—	—
Diptera	0.35	0.32	0.25	0.27	−0.25	—	—	—

[a] If $|r| \geq 0.33$, $P < 0.01$; if $0.33 > |r| \geq 0.27$, $P < 0.05$; if $0.27 > |r| \geq 0.23$, $P < 0.10$.

studied by Fowler (1985). Pearson product-moment coefficients arrayed above the principal diagonal variables not significantly correlated. Variables as defined in Table A9.

Fish abundance							
Brook Trout				Rainbow Trout			
Adult		Y-O-Y		Adult		Y-O-Y	
Biomass	Density	Biomass	Density	Density	Biomass	Density	Biomass
0.48	-0.44	—	—	0.43	0.50	0.37	0.33
-0.51	-0.53	—	—	0.50	0.61	—	0.31
-0.47	-0.44	—	—	0.30	0.40	—	—
-0.40	-0.38	—	—	0.62	0.74	—	0.42
0.39	0.53	—	—	-0.47	-0.42	-0.41	-0.25
0.46	0.40	—	—	-0.53	-0.58	-0.24	-0.30
—	—	0.34	0.34	-0.34	-0.32	—	—
—	—	0.30	0.31	-0.35	-0.36	-0.23	—
•	0.88	—	—	-0.61	-0.58	-0.32	-0.29
0.89	•	—	—	-0.63	-0.60	-0.35	-0.29
0.43	0.44	•	0.99	—	—	—	—
0.44	0.43	0.99	•	—	—	—	—
-0.73	-0.71	-0.48	-0.49	•	0.95	0.53	0.52
-0.73	-0.72	-0.47	-0.48	0.98	•	0.52	0.58
-0.54	-0.56	-0.40	-0.40	0.69	0.70	•	0.75
-0.54	-0.56	-0.40	-0.40	0.69	0.70	0.99	•
-0.40	-0.39	-0.23	-0.23	0.40	0.45	0.56	0.57
-0.40	-0.39	-0.23	-0.23	0.40	0.45	0.56	0.57
-0.28	-0.25	—	—	0.49	0.53	0.45	0.48
-0.27	-0.24	—	—	0.48	0.52	0.44	0.47
—	—	—	—	—	—	0.23	0.23
—	—	—	—	—	—	0.23	0.23
-0.68	-0.70	-0.49	-0.49	0.76	0.72	0.62	0.62
-0.69	-0.70	-0.49	-0.49	0.76	0.76	0.60	0.61
—	—	—	—	0.29	0.32	0.33	0.32
—	—	—	—	—	—	—	—
—	—	—	—	0.39	0.37	0.57	0.57
—	—	—	—	—	—	—	—
—	—	—	—	0.23	0.25	0.29	0.27
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	0.36	0.37	0.37	0.35
—	—	—	—	0.23	0.25	—	—

Table A10. *Continued.*

Fish abundance (*continued*)							
Brown trout		Longnose dace		Creek chub		Sculpins	
Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass
0.23	0.30	0.36	0.36	—	—	0.48	0.49
—	0.34	0.69	0.61	—	—	0.36	0.39
—	0.24	0.42	0.40	—	—	0.27	0.30
—	0.43	0.83	0.69	—	—	0.32	0.37
-0.37	-0.31	—	—	-0.31	-0.31	-0.61	-0.57
-0.18	-0.33	-0.51	-0.48	—	—	-0.28	-0.27
—	—	—	—	—	—	-0.27	-0.24
—	—	-0.26	-0.25	—	—	-0.30	-0.29
-0.22	-0.29	-0.25	—	—	—	-0.52	-0.51
-0.24	-0.30	-0.25	—	—	—	-0.55	-0.54
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	0.44	0.49	0.38	—	—	0.64	0.61
0.30	0.57	0.57	0.47	0.24	0.24	0.57	0.55
0.45	0.44	—	—	—	—	0.56	0.51
0.31	0.53	—	—	—	—	0.47	0.47
•	0.85	—	—	—	—	0.41	0.24
—	•	—	—	—	—	0.42	0.30
0.28	0.28	•	0.93	—	—	—	—
0.28	0.28	0.99	•	—	—	—	—
—	—	—	—	•	—	—	—
—	—	—	—	—	•	—	—
0.45	0.45	—	—	—	—	•	0.95
0.43	0.43	0.24	0.23	—	—	0.99	•
0.24	0.24	—	—	—	—	—	—
—	—	—	—	—	—	—	—
0.35	0.35	0.23	0.23	—	—	0.29	0.27
—	—	—	—	—	—	-0.28	-0.28
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	—	—	0.30	0.27
—	—	—	—	—	—	—	—

Invertebrate density								
Oligochaeta	Gastropoda	Odonata	Ephemeroptera	Plecoptera	Coleoptera	Megaloptera	Trichoptera	Diptera
0.49	—	0.24	—	0.38	—	—	0.39	0.39
—	—	—	—	0.23	—	—	—	0.23
—	—	—	—	0.29	—	—	—	—
—	—	—	—	—	—	—	—	—
-0.47	—	-0.38	0.29	—	—	—	-0.30	-0.30
—	—	—	—	-0.30	0.27	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	-0.25	—	—	—	—
—	—	-0.27	—	—	—	—	—	-0.22
—	—	-0.24	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	0.48	-0.25	—	—	—	0.24	0.33
—	—	0.42	—	—	—	—	—	—
0.39	—	0.76	—	0.33	—	—	0.56	0.53
—	—	0.52	—	—	—	—	0.27	0.24
0.58	—	0.37	—	—	—	—	0.30	—
0.58	—	0.37	—	—	0.23	—	0.30	—
0.47	—	0.34	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
•	—	—	—	—	—	—	—	—
—	•	—	—	—	—	—	—	—
0.40	—	•	—	—	—	—	—	—
0.32	—	—	•	—	0.33	0.28	—	0.71
0.61	—	0.30	0.55	•	0.35	—	0.46	0.62
0.52	—	0.44	0.54	0.50	•	—	0.42	0.49
—	—	—	—	—	—	•	—	—
0.64	—	0.70	—	0.38	0.43	—	•	0.46
0.71	—	—	0.62	0.61	0.66	—	—	•

Table A11. Results of multiple regression analysis, as regression coefficients and other statistics,[a] relating brook trout abundance (as $\log_{10}$ density, no./ha, and $\log_{10}$ biomass, kg/ha) to physicochemical and biological variables in seven SBRP streams surveyed by Fowler (1985).

Variable or statistic	Physicochemical variables only		Physicochemical and biological variables	
	Density	Biomass	Density	Biomass
Intercept (β_0)	7.90	2.13	7.5	0.30
Length	0.017	—	—	—
Width	-0.086	-0.24	-0.161	—
Flow	0.077	0.10	0.027	—
Gradient	—	—	—	0.069
Elevation	0.00083	—	—	—
pH	-1.11	—	-0.647	—
Alkalinity	—	-0.11	—	—
Abundance[b]				
Rainbow trout	—	—	-0.016	-0.0347
Brown trout	—	—	-0.0048	—
Sculpins	—	—	—	-0.0502
Gastropoda	—	—	-0.6629	—
Plecoptera	—	—	0.0118	—
Odonata	—	—	—	0.0384
F[c]	12.03	21.74	47.23	39.88
R^2	0.70	0.70	0.87	0.76

[a] All listed coefficients statistically significant ($P \leq 0.05$); *dashes* indicate pairs of variables not significantly correlated.
[b] For fishes, abundance in same units as brook trout (no. / ha.); for invertebrates, no. / m^2.
[c] All regressions highly significant overall ($P \ll 0.01$).

Table A12. Mean ($\bar{x}$), standard deviation (SD), median, minimum, and maximum values of variables measured in 138 streams (n = 136 for invertebrate densities, n = 129 for pH, alkalinity, and hardness) by the North Carolina Wildlife Resources Commission (1983).

Variable	$\bar{x}$	SD	Median	Minimum	Maximum
Physicochemical					
Width (m)	4.1	1.6	3.7	1.5	9.8
Flow (cubic feet / s)	10.9	6.7	8.0	3.0	35.0
Gradient (%)	2.1	0.67	2.0	1.0	3.0
Cover (%)	3.0	0.7	3.0	1.0	4.0
Elevation (m)	964.1	232.2	948.5	427.0	1,647.0
pH	6.91	0.34	7.0	6.5	8.0
Alkalinity (mg / L)	11.7	4.9	8.6	4.3	34.2
Hardness (mg / L)	19.0	5.8	17.1	17.1	51.3
Fish density (no. / ha)					
Brook trout	477.3	546.8	301.5	7.0	2,662.0
Rainbow trout	105.6	289.0	0	0	1,892.0
Total Y-O-Y[a]	344.9	416.8	212.5	0	2,372.0
Brown trout	33.9	98.8	0	0	560.0
Longnose dace	42.7	143.4	0	0	891.0
Blacknose dace[b]	213.4	600.9	0	0	4,429.0
Rosyside dace[c]	83.1	282.2	0	0	1,972.0
Creek chub	24.0	88.0	0	0	678.0
Bluehead chub[d]	29.8	138.1	0	0	1,105.0
Sculpins	20.1	381.9	0	0	2,141.0
Stoneroller[e]	30.9	173.6	0	0	1,630.0
Greenside darter[f]	0.1	1.7	0	0	20.0
Striped jumprock[g]	2.1	14.7	0	0	129.0
Invertebrate density (no. / square foot)					
Oligochaeta	0.25	0.66	0	0	4.0
Gastropoda	0.63	2.13	0	0	19.0
Hemiptera	0.07	0.31	0	0	2.0
Odonata	0.26	0.77	0	0	6.0
Ephemeroptera	21.56	24.22	13.0	1.0	160.0
Plecoptera	6.71	6.64	4.5	0	33.0
Coleoptera	1.38	2.89	0	0	18.0
Megaloptera	0.09	0.45	0	0	3.0
Trichoptera	17.0	26.26	8.0	0	193.0
Diptera	7.39	11.69	5.0	0	115.0

[a] Salmonids.
[b] *Rhinichthys atratulus.*
[c] *Clinostomus funduloides.*
[d] *Nocomis leptocephalus.*
[e] *Campostoma anomalum.*
[f] *Etheostoma blennioides.*
[g] *Moxostoma rupiscartes.*

Table A13. Statistically significant[a] correlations between variables measured in 138 SBRP streams by arrayed above the principal diagonal (indicated by *bullets*), Spearman rank coefficents below.

Variable	Physicochemical variables							
	Width	Flow	Gradient	Cover	Elevation	pH	Alkalinity	Hardness
Physicochemical								
Width	•	-0.81	—	—	—	0.21	—	—
Flow	0.78	•	—	0.15	—	0.22	—	—
Gradient	—	—	•	0.30	—	—	—	—
Cover	—	0.24	0.32	•	0.15	-0.17	—	—
Elevation	—	-0.14	—	0.19	•	-0.31	-0.30	—
pH	0.21	0.15	—	-0.16	-0.34	•	0.55	0.32
Alkalinity	—	—	-0.20	—	-0.33	0.50	•	0.49
Hardness	—	—	—	—	—	0.32	0.31	•
Fish density								
Brook trout	-0.45	-0.35	—	0.21	0.36	-0.24	-0.20	—
Rainbow trout	—	—	—	—	—	—	—	—
Y-O-Y[b]	-0.32	-0.26	—	—	—	—	—	—
Brown trout	0.45	0.36	—	—	-0.18	0.25	0.15	—
Longnose dace	0.39	0.36	—	—	—	0.31	0.31	0.21
Blacknose dace	0.16	—	-0.26	-0.25	-0.22	0.45	0.49	0.34
Rosyside dace	—	—	-0.28	-0.26	-0.34	0.33	0.30	—
Creek chub	—	—	-0.28	-0.25	-0.40	0.23	0.24	—
Bluehead chub	—	—	-0.26	-0.23	-0.35	0.26	0.29	—
Sculpins	—	—	—	-0.23	—	0.33	0.42	0.33
Stoneroller	0.27	0.29	—	—	—	0.38	0.33	0.27
Greenside darter	—	—	—	-0.16	—	—	—	—
Striped jumprock	—	—	—	—	-0.22	—	—	—
Invertebrate density								
Oligochaeta	0.21	0.19	—	—	—	—	0.17	—
Gastropoda	—	—	—	—	—	0.36	0.39	0.21
Hemiptera	—	—	—	—	—	—	—	—
Odonata	-0.18	-0.19	—	—	—	—	—	—
Ephemeroptera	0.22	0.22	—	—	-0.20	0.42	0.54	0.18
Plecoptera	—	—	—	0.15	—	0.21	0.24	—
Coleoptera	—	—	-0.14	-0.16	-0.26	0.41	0.28	—
Megaloptera	—	—	—	—	—	0.19	0.30	—
Trichoptera	—	—	-0.16	-0.23	-0.17	0.45	0.48	0.26
Diptera	—	—	-0.16	—	—	0.27	0.41	—

[a] If $|r| \geq 0.21$, $P < 0.01$; if $0.21 > |r| \geq 0.16$, $P < 0.05$; if $0.16 \geq 0.14$, $P < 0.10$.
[b] Salmonids.

The North Carolina Wildlife Resources Commission (1983). Pearson product-moment coefficients *Dashes* indicate pairs of variables not significantly correlated. Variables as defined in Table A12.

Fish density										
Brook trout	Rainbow trout	Y-O-Y	Brown trout	Longnose dace	Blacknose dace	Rosyside dace	Creek chub	Bluehead chubTpins	Scul- roller	Stone-
-0.41	—	-0.31	0.16	0.29	—	—	—	—	—	0.25
-0.31	—	-0.27	0.14	0.39	—	—	—	—	—	0.40
—	—	—	—	—	-0.19	-0.18	-0.19	-0.17	—	—
0.17	—	—	—	—	-0.27	-0.14	-0.29	-0.18	-0.17	—
0.32	—	—	-0.17	—	—	-0.28	-0.24	-0.24	—	—
-0.24	—	—	0.23	0.20	0.31	0.22	—	—	0.39	0.29
-0.16	—	—	—	0.28	0.47	0.36	—	—	0.58	0.31
—	0.19	—	—	0.21	0.27	—	—	—	0.46	—
•	-0.19	0.69	-0.21	-0.17	—	—	-0.17	—	—	—
-0.34	•	0.19	—	—	—	—	—	—	—	—
0.65	—	•	—	—	—	—	-0.14	—	—	—
-0.44	—	-0.21	•	—	—	—	—	—	—	0.15
-0.31	0.15	—	0.42	•	—	—	—	—	0.26	0.45
-0.25	0.14	—	0.19	0.34	•	0.46	0.34	—	0.50	—
-0.29	—	-0.20	0.18	—	0.52	•	0.52	0.41	0.18	—
-0.27	—	-0.18	0.22	—	0.35	0.78	•	0.41	—	—
-0.30	—	—	0.23	—	0.27	0.58	0.66	•	—	—
—	—	—	0.18	0.28	0.52	0.18	—	—	•	—
-0.33	0.11	-0.28	—	—	—	0.31	—	0.26	—	•
—	—	—	—	0.21	—	—	—	—	—	0.29
-0.20	—	-0.19	—	—	—	0.23	0.20	0.30	—	—
—	—	—	0.22	0.19	—	—	—	—	—	0.14
—	0.15	—	0.19	0.23	0.35	0.30	—	—	0.28	0.31
—	—	—	—	—	—	0.16	—	—	—	0.16
0.25	—	0.23	—	—	—	—	—	—	—	—
-0.22	—	-0.16	0.22	0.23	0.22	0.24	0.23	0.25	0.15	0.22
—	—	—	—	—	—	0.17	0.15	0.20	—	—
-0.22	—	—	0.21	0.15	0.21	0.33	0.32	0.27	—	0.16
-0.21	—	—	—	0.28	0.25	0.31	—	0.16	0.20	0.32
—	—	—	—	0.19	0.46	0.41	0.28	0.31	0.35	0.20
—	—	—	—	0.20	0.23	0.25	0.17	0.21	0.17	0.18

Table A13. *Continued.*

		Invertebrate density									
Greenside darter	Striped jumprock	Oligochaeta	Gastropoda	Hemiptera	Odonata	Ephemeroptera	Plecoptera	Coleoptera	Megaloptera	Trichoptera	Diptera
0.15	—	0.20	—	—	-0.16	0.22	—	—	—	0.17	—
0.25	—	—	—	—	-0.17	0.21	—	—	—	—	—
—	—	—	—	—	-0.16	—	—	—	—	—	—
-0.24	—	—	—	—	—	—	0.18	—	—	-0.23	—
—	-0.27	—	—	—	—	-0.30	—	-0.24	—	—	—
—	—	—	0.27	—	—	0.36	0.17	0.45	0.22	0.49	0.18
—	—	—	0.54	0.21	—	0.50	0.16	0.39	0.39	0.57	0.34
—	—	—	0.27	—	—	—	—	0.15	—	0.38	—
—	—	—	—	—	0.32	-0.116	—	-0.16	—	-0.16	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	0.32	—	—	—	—	0.15	—
—	—	—	—	—	—	0.20	—	—	—	—	—
0.15	—	—	—	—	—	—	—	0.16	—	0.15	—
—	—	—	0.48	0.30	—	—	—	0.27	0.36	0.46	0.28
—	0.17	—	0.44	0.28	—	0.19	0.18	0.46	0.39	0.28	—
—	—	—	—	0.18	—	0.15	—	—	—	—	—
—	0.15	—	—	—	—	—	—	—	—	—	—
—	—	—	0.42	0.20	—	0.20	—	—	0.32	0.52	0.28
—	—	—	—	—	—	—	—	—	—	—	—
•	—	—	—	—	—	—	—	—	—	—	—
—	•	—	—	—	—	—	—	—	—	—	—
—	—	•	—	—	0.27	—	—	—	—	—	—
—	—	—	•	0.35	0.17	0.32	0.25	0.27	0.57	0.49	0.27
—	—	—	—	•	—	0.28	0.22	—	0.27	0.23	—
—	—	—	—	—	•	—	—	—	—	—	—
—	—	0.16	0.32	0.16	—	•	0.46	0.40	0.32	0.46	0.29
—	—	—	0.19	0.22	—	0.47	•	0.30	0.26	0.29	0.32
—	—	—	0.30	—	—	0.39	0.34	•	0.31	0.40	0.19
—	—	—	0.33	—	—	0.28	0.23	0.33	•	0.35	0.73
—	—	0.17	0.30	0.16	—	0.59	0.40	0.39	0.27	•	0.33
—	—	0.24	0.24	—	—	0.44	0.40	0.28	0.32	0.47	•

Table A14. Results of multiple regression analysis, as regression coefficients and other statistics,[a] relating brook trout abundance (as $\log_{10}$ density, no./ha) to physicochemical and biological variables in SBRP streams surveyed by the North Carolina Wildlife Resources Commission (1983). Variables as defined in Table A12.

Variable or statistic	Brook trout streams, physicochemical variables only	All streams, physicochemical and biological variables
Intercept (β_0)	2.406	1.927
Length	-0.007	—
Width	-0.131	-0.155
Cover	0.239	0.232
Elevation	0.001	0.001
Density[b]		
Rainbow trout	—	-0.160
Brown trout	—	-0.181
Striped jumprock	—	-0.354
Odonata	—	-0.141
Megaloptera	—	-0.203
n	81	129
F[c]	11.95	21.43
R^2	0.39	0.59

[a] All listed coefficients statistically significant ($P \leq 0.05$); *dashes* indicate pairs of variables not significantly correlated.
[b] For fishes, log density (no./ha.); for invertebrates, no./m^2.
[c] Both regressions highly significant overall ($P << 0.01$).

Table A15. Results of multiple regression analysis,[a] as regression coefficients and other statistics,[b] relating brook trout abundance to other variables in SBRP streams. Variables as defined in Tables A6, A9, and A12.

Variables and statistics	All streams and data	Trout[c] streams	Brook trout streams[d] and physicochemical variables only
Intercept (β_0)	2.281	-4.843	1.53
Gradient	-2.873	-1.768	—
(Gradient)^2	3.359	1.923	0.101
(Gradient)^3	-0.852	-0.440	—
(Width)^2	0.570	-0.268	—
(Width)^3	0.110	—	-0.134
Elevation	0.179	2.431	1.952
pH	—	-0.779	-1.288
(Rainbow trout density)^3	-0.005	-0.005	—
n		256	253,165
F[b]	32.15	—	38.83
R^2	0.48	0.53	0.44

[a] All listed coefficients statistically significant ($P < 0.05$); *dashes* indicate pairs of variables not significantly correlated.
[b] All regressions highly significant overall ($P << 0.01$).
[c] Containing brook trout, rainbow trout, or both.
[d] Containing brook trout but not rainbow trout.

Table A16. Statistically significant[a] correlations between brook trout abundance, the abundance of all other fishes combined, and physicochemical attributes of seven SBRP streams ($n = 56$) studied by Fowler (1985). Pearson product-moment coefficients arrayed above the principal diagonal (indicated by *bullets*), Spearman rank coefficients below. *Dashes* indicate pairs of variables not significantly correlated. Variables as defined in Table A9.

	Brook trout		Other species (total)		Stream size			Other			
	Density	Biomass	Density	Biomass	Width	Depth	Flow	Gradient	Elevation	pH	Alkalinity
Brook trout											
Density	•	0.88	-0.61	-0.59	-0.51	-0.47	-0.40	0.39	0.46	—	—
Biomass	0.89	•	-0.65	-0.61	-0.53	-0.44	-0.38	0.53	0.40	—	—
Other species (total)											
Density	-0.72	-0.73	•	0.89	0.51	0.35	0.54	-0.60	-0.45	-0.33	-0.36
Biomass	-0.74	-0.74	0.98	•	0.63	0.43	0.73	-0.49	-0.57	-0.33	-0.38
Stream size											
Width	-0.57	-0.59	0.48	0.51	•	0.79	0.85	—	-0.70	—	-0.27
Depth	-0.46	-0.42	0.39	0.43	0.84	•	0.57	—	-0.65	—	—
Flow	-0.46	-0.41	0.40	0.46	0.82	0.76	•	—	-0.58	—	—
Other											
Gradient	0.49	0.61	-0.51	-0.48	-0.25	—	—	•	—	—	—
Elevation	0.50	0.37	-0.53	-0.58	-0.67	-0.64	0.59	—	•	—	0.52
pH	—	—	-0.35	-0.35	—	—	0.29	—	—	•	0.86
Alkalinity	—	—	-0.41	-0.41	-0.46	-0.39	-0.30	-0.23	0.66	0.51	•

[a] If $|r| \geq 0.33$, $P \leq 0.01$; if $0.33 > |r| \geq 0.27$, $P < 0.05$; if $0.27 > |r| \geq 0.23$, $P < 0.10$.

Table A17. Statistically significant[a] correlations between brook trout abundance, the abundance of all other fishes combined, and physicochemical attributes in 138 SBRP streams surveyed by the North Carolina Wildlife Resources Commission (1983). Pearson product-moment coefficients arrayed above the principal diagonal (indicated by *bullets*), Spearman rank coefficients below. *Dashes* indicate pairs of variables not significantly correlated. Variables as defined in Table A12.

	Fish density		Stream size		Other				
Variable	Brook trout	Others	Width	Flow	Gradient	Elevation	pH	Alkalinity	Hardness
Fish density									
Brook trout	•	-0.20	-0.41	-0.32	—	0.32	-0.23	-0.16	—
Other species (total)	-0.49	•	—	—	-0.19	-0.22	0.47	0.63	0.38
Stream size									
Width	-0.45	0.17	•	0.81	—	—	0.21	—	—
Flow	-0.35	—	0.78	•	—	—	0.22	—	—
Other									
Gradient	—	-0.19	—	—	•	—	—	—	—
Elevation	0.36	-0.34	—	—	—	•	-0.31	-0.30	—
pH	-0.27	0.49	0.21	0.15	—	-0.34	•	0.55	0.31
Alkalinity	-0.20	0.53	—	—	-0.21	-0.34	0.50	•	0.49
Hardness	—	0.35	—	—	—	—	0.32	0.31	•

[a] If $|r| \geq 0.21$, $P < 0.01$; if $0.21 > |r| \geq 0.16$, $P < 0.05$; if $0.16 > |r| \geq 0.14$, $P < 0.10$.

Table A18. Statistically significant[a] correlations (n = 56) between mean brook trout weight (biomass and density) and other variables in seven SBRP streams surveyed by Fowler (1985). *Dashes* indicate pairs of variables not significantly correlated. Variables as defined in Table A9.

Variable	Coefficient[b] $r_{p'}$	r_{SD}
Flow	0.34	—
Gradient	0.30	0.38
Elevation	−0.28	−0.29
Brook trout density	−0.22	—
Brook trout biomass (adult)	0.23	—
Rainbow trout biomass (adult)	—	0.23
Rainbow trout biomass (Y-O-Y)	0.35	—
Longnose dace density	0.23	—
Longnose dace biomass	—	0.32
Gastropod abundance	0.32	—

[a] If $|r| \geq 0.33$, $P \leq 0.01$; if $0.33 > |r| \geq 0.27$, $P < 0.05$; if $0.27 > |r| \geq 0.23$, $P < 0.10$.
[b] $r_{p'}$, Pearson product-moment; r_{SD}, Spearman rank.

Table A19. Results of principal components regression analysis[a] relating brook trout abundance to physicochemical variables and rainbow trout abundance[b] in SBRP streams. Data from North Carolina Wildlife Resources Commission (1983), Fowler (1985), and U.S. National Park Service (Parker MS).

Variables and statistics	Factor 1	2	3	4	5
Standardized scoring coefficients[c]					
Width	0.371	0.203	0.645	−0.554	0.642
Elevation	0.072	−0.621	0.440	0.653	0.405
Gradient	0.370	−0.134	−0.791	<0.001	0.729
pH	−0.431	0.263	−0.003	0.216	1.142
Rainbow trout density	0.269	0.492	0.075	0.938	−0.166
Variability explained					
Proportion	0.37	0.26	0.16	0.12	0.08
Cumulative total	0.37	0.64	0.80	0.92	1.00
Regression coefficients (β_0 = 0.645)	—	−0.126	−0.028	—	−0.015

[a] n = 256, F = 49.00 ($P < 0.01$), R^2 = 0.37.
[b] All variables except pH $\log_{10}$ transformed.
[c] Weightings of the variables in each factor after transformation to standard deviation units.

Table A20. Results of principal components regression analysis[a] relating brook trout abundance to physicochemical variables[b] in SBRP streams. Data from North Carolina Wildlife Resources Commission (1983), Fowler (1985), and U.S. National Park Service (Parker MS).

Variables and statistics	Factor 1	2	3	4
Standardized scoring coefficients[c]				
Width	0.503	0.821	−0.036	0.259
Elevation	0.579	−0.325	0.707	0.243
Gradient	0.602	−0.421	−0.617	0.283
pH	−0.855	−0.028	0.024	0.517
Variability explained				
Proportion	0.42	0.24	0.22	0.12
Cumulative total	0.42	0.66	0.88	1.00
Regression coefficients (β_0 = 0.714)	0.099	−0.069	0.024	−0.029

[a] n = 165, F = 30.34 (P < 0.01), R^2 = 0.43.
[b] All variables except pH $\log_{10}$ transformed.
[c] Weightings of the variables in each factor after transformation to standard deviation units.

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